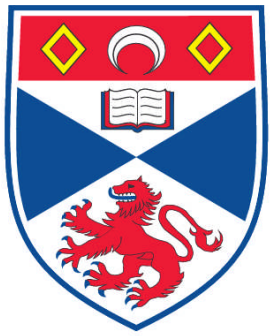
MEASUREMENT OF CHANGES IN MARINE BENTHIC ECOSYSTEM FUNCTION FOLLOWING PHYSICAL DISTURBANCE BY DREDGING

Wan Mohd Rauhan Wan Hussin

A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews



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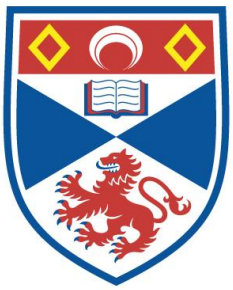
Measurement of changes in marine benthic ecosystem function following physical disturbance by dredging

by

WAN MOHD RAUHAN WAN HUSSIN

A thesis submitted in accordance with the requirements of the University of St Andrews for the degree of Doctor of Philosophy



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Alhamdu lillah, syukur kepada Allah S.W.T kerana dengan izinNya, dengan berkat kekasih-Nya Nabi Muhammad S.A.W, dengan berkat Guru-Guru ku, dengan karamah Ibu dan hikmah Bapa ku, pengajian ini dapat disempurnakan dengan jayanya.

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Abstract

Measuring the impact of physical disturbance on macrofaunal communities and sediment composition is important given the increase demand for the exploitation and disturbance of marine ecosystems. The aim of the present investigation was to provide a comprehensive study about the extent to which the disturbance (especially aggregate dredging) may affect benthic ecosystem function.

The first part of the thesis concerns a field investigation of the impacts of dredging on the benthic community and related ecosystem function which was measured by different approaches including traditional methods based on benthic community structure and a more novel approach based on the functional traits of benthic organisms. The assessment was done by comparing dredged sites (Area 222, southeast England) with nearby undisturbed reference sites from the years 2001 to 2004 and in 2007. In general, low dredging intensity did not appear to impose great impacts on the benthic community and related ecosystem function compared to the higher intensity activity. Most of the analyses suggested that the community at the high dredging intensity site had yet to recover at the end of this study period. Among many factors related to the recovery of the benthic community was sediment composition where gravel deposits appeared to support a faster biological recovery. Meanwhile, the recovery of species with specific traits, such as tube-building and filter feeding also indicate a faster recovery for the whole community.

The experimental work to determine different impacts of *Hediste diversicolor* on its surrounding depending on its relative size is discussed in Appendix 1.

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Chapter 1: Introduction

Humans exert a great impact on the marine environment and marine ecological processes, and often these impacts are harmful to marine species and to humans themselves (Balmford et al., 2002; Wackernagel et al., 2002). Food supply and economic gain are the main reason behind the exploitation of marine resources. Unrestricted activity however can be associated with catastrophic effect where the ecosystem is negatively affected (Kaiser et al., 2005). Human activities modify the marine environment through habitat destruction, removal of organisms, and change to physical structures. The activities that cause obvious and widespread effects on the marine system, among many others, include commercial fishing (Collie et al., 2000; Kaiser et al., 2005; Tillin et al., 2006) and marine aggregate dredging (Newell et al., 1998; Boyd and Rees 2003; Boyd et al., 2005; Robinson et al., 2005; Smith et al., 2006). Due to the increase in the size and weight of gear (Hall, 1994) and increased demand on resources, both fishing and aggregate dredging have caused an increasing concern over their impact on benthic communities. The concern is highly relevant given the fact that benthic communities play a central role in transferring materials from primary production to higher levels in the food web, including fish (Newell et al., 1998).

1.1 Benthic community structure

The main themes that are studied by benthic ecologists include ecosystem function, community structure and the role played by individuals in the environment. In a community, the survival and reproduction of benthic fauna are important controls on the change of population over time. Therefore, studies concerning ecosystems, communities and populations have to take into account the survival and reproduction of the relevant populations (Pineda et al., 2009).

The shaping of benthic communities under highly variable environmental conditions depends on the interaction between the community and its environment (Newell et al., 1999; Pineda et al., 2009). In contrast, the shaping of the community under more stable conditions is dependent on biological interactions (Newell et al., 1999). Different environmental conditions are associated with different dominant species with '*r-strategists*' dominating unstable environments while '*K-strategists*' are dominant species in stable environments (Pineda et al., 2009). The '*r-strategists*' or

‘opportunist’ species are characterised by small-bodied fauna, with high fecundity, fast growth rate and high mortality (Pianka, 1970). In unstable environments or in disturbed habitats, the benthic community is dominated by ‘mobile opportunists’ species which have high mobility and can quickly colonise vacant habitats with large populations (Grassle and Grassle, 1974; Osman, 1977). In contrast, ‘*K-strategists*’ control the community in the stable environments. These species display an ‘equilibrium strategy’ reaching the maximum ability to compete in an environment with limited space for settlement and colonisation by many competing species (Newell et al., 1999). ‘*K-strategists*’ species use most of their resources for non-reproductive processes such as growth and defence against predators (Gadgil and Bossert, 1970; McCall, 1976).

Community composition of benthic infauna is controlled by biological interactions at the sediment surface. For example, surface-dwelling species facilitate colonisation by other species that would not normally inhabit the sediment surface (Newell et al., 1998). Another example is that suspension feeding activity by mussels produces consolidated particles which promote the presence of deposit feeder and the burrowing polychaete, *Amphitrite.* The presence of burrows subsequently helps to provide shelter for other species (Newell, 1979). Burrowing or bioturbation activity by the organism reworks the compact sediments and may enhance carbon and nutrient cycling and draw these materials deeper down into the sediments and also transfer the materials to the sediment-water interface (Meysman et al., 2006; Snelgrove and Butman, 1994). However, bioturbatory activity also can cause adverse effect to other species. The unstable seabed conditions caused by the reworking of sediments by deposit feeding species prevents filter feeders becoming established because these species cannot tolerate a seadbed surface with the continuous resuspension of particles. This phenomenon, known as trophic group amensalism, was first described by Rhoads and Young (1970).

In modern ecological theory, bioturbators (especially burrowers) are recognised as ‘ecosystem engineers’ based on the fact that their modification of physical environment strongly affects other organisms (Jones et al., 1994). The loss of such species may be detrimental to the entire biologically-accommodated community although there are some individual species that are tolerant to environmental changes (Newell et al., 1998). Another example of an ‘ecosystem engineering’

species is the reef building polychaete *Sabellaria spinulosa* which provides a complex structural habitat associated with high biodiversity of species that would not be present without this structure (Brown et al., 2001; Dubois et al., 2002). Therefore, disturbance of this community may impose a greater impact than of some other communities, and the removal of engineering species may mean the environment needs longer time to achieve full biological recovery (Newell et al., 1998). Other than the keystone species, habitats dominated by '*K-strategists*' species may also take a longer time to recover compared to the habitats dominated by '*r-strategists*' species (Newell et al., 1998).

1.2 Use of benthic fauna as indicators for disturbance

Benthic infaunal communities demonstrate the ability to change in a predictable manner along gradients of natural and anthropogenic stresses (Pearson and Rosenberg, 1978; Rhoads and Germano, 1986; Swartz et al., 1986; Dauer, 1993; Tapp et al., 1993; Weisberg et al., 1997). Benthic infauna have been one of the most common organismal groups used as indicators for assessing environmental quality in marine environments due to their diversity and known characteristics such as limited mobility (meaning they are unable to avoid the environmental changes as most pelagic fauna can) (Gray, 1979) and long life spans of up to several years (Nilsson and Rossenberg, 1997). Another factor that makes the benthic infauna suitable indicator organisms is their sensitive response to various environmental stressors due to their physiological tolerances, feeding mechanisms and trophic interactions (Pearson and Rosenberg, 1978; Rhoads et al., 1978). Although benthic infauna exhibits many advantages in environmental assessment, the use of these organisms can also be problematic. For instance, the methods used in the analysis (sampling, processing and identification) need a great deal of logistic effort and can be very expensive (Nilsson and Rossenberg, 1997).

Measuring the changes in benthic community composition in different habitats and at different times is usually conducted with high precision by benthic scientists. Yet, this rigorous work is not always translated when it comes to linking the change in benthic communities with environmental conditions where often the assessment is based on subjective interpretation (O'Connor and Dewling, 1986). It is not surprising when this subjective aspect causes frustration among environmental managers and policy makers, as the interpretation among scientists varies. Therefore, to reduce

subjectivity in the interpretation, Smith et al. (2001) and Borja et al. (2008) suggested a protocol where benthic data assessment was divided into 3 categories: 1) Measurement of community structure on the level of species-abundance data such as Simpson index (Simpson, 1949) and Taxonomic Distinctness (Warwick and Clark, 1993). This type of measurement is not suitable in all cases since benthic fauna respond differently to different types of stresses. Thus it is important to apply different measures to quantify different levels of response (Pearson and Rosenberg, 1978). 2) By combining multiple measures of community response into a single index (multimetric index), the response of benthic fauna to the different levels of environmental stress can be measured more effectively (Nelson, 1990; Engle et al., 1994; Weisberg et al., 1997). The index includes the Biological Quality Index (BQI) (Jeffrey et al. 1985), the Benthic Condition Index (BCI) (Paul et al., 2001) and the AMBI (Borja et al., 2000; 2003). 3) The use of multivariate analysis to describe the compositional pattern of benthic community (Field et al., 1982). Multivariate space is more sensitive to any perturbation compared to the univariate methods based on assemblage metrics (Norris, 1995). Nevertheless, the interpretation from a multivariate approach can be very complex and thus difficult to transmit to environment managers (Gerritsen, 1995).

An easily interpreted method of measuring environmental condition is required by many bodies involved in ecosystem study and management. Combining multivariate data into a single numeric score (or category) might be one approach to settle this issue. This integrative approach allows the non-ecologists to interpret the outcome in a more straight-forward way within a system categorised into ‘good’ and ‘bad’ conditions (Diaz et al., 2004).

1.3 Biodiversity and ecosystem function

The Convention on Biological Diversity (CBD) defined biodiversity as “variety among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and ecosystems (Kaiser et al., 2005). Based on this definition, Gaston and Spicer (2004) suggested the word ‘living’ be changed to ‘living and those that ever lived’ to consider past forms and their lingering effects (the vast majority of life). This is relevant to the present study, for example where tube worms create raised beds, the organic enrichment stimulated by

fragmented remains of fauna, and also the changes in sediment composition due to benthic organisms' activities.

Ecological functions can be defined as transformation in an ecosystem involving ecological and evolutionary processes, including gene flow, disturbance, and nutrient cycling. The study of ecosystem functioning involves understanding how components of ecosystems operate and how this is related to species diversity and change over space and time. For many years, ecologists have studied the ecological functioning (or role) of individual species. Nevertheless, the study of the influence of biodiversity on overall ecological function is still relatively new. This field of study is complex and needs further investigation (Noss, 1990; Loreau et al., 2001; Solan et al., 2006).

Species richness, the number of species in an area, is the most common way to measure biological diversity in assessing ecosystem function (Magurran, 2004; Tilman, 1997). The use of this measurement to relate to the overall diversity of a system may be limited since richness does not take into account species evenness, the relative distribution of species in the given community (Magurran, 2004). Other measures such as using functional trait richness to determine biodiversity effects on ecosystem function are more complex but perhaps represent a natural assemblage better. In marine benthic systems, functional trait richness is related to the various ways organisms may affect the sediment environment through their feeding, movement, respiratory behaviour; and this probably provides the most appropriate assessment of biodiversity and ecosystem function (Bengtsson, 1998).

1.3.1 Changes in biodiversity and ecosystem function

Many ecosystems around the world are undergoing a striking change of species composition as a result of human activities (Balmford et al., 2002; Wackernagel et al., 2002). This change has reduced the diversity of species in many ecosystems. Changes in species composition, species richness and/or functional traits impacts on the efficiency of functioning of an ecosystem (Bengtsson, 1998), as the number and type of species in an ecosystem each have their specific traits (Symstad et al., 2003). For example, species traits such as feeding, burrowing and movement can directly mediate energy and material fluxes or in some cases change abiotic conditions (e.g. disturbance, climate and limiting resources) that regulate functional rates (Heisse et al., 2007). Species losses occur locally, nationally and globally, hence this

phenomenon will reduce the genetic diversity (Hooper et al., 2005) and ecosystem function (Ehrlich and Mooney, 1983). The consequences of mass species loss to human activity are potentially huge; including changes in functioning of ecosystems that provide crucial services such as nutrient cycling and photosynthesis. This would have a direct effect on material goods, causing a loss of crops, natural resources, and even medicines. There would also be a loss of non-market values such as the aesthetic beauty of biodiversity. The scientific challenge is to predict the importance of a reduction in biodiversity, to ultimately improve environmental policy in protecting habitats and species richness (Hooper et al., 2005; Fischer and Young, 2007).

The biodiversity concept can also be applied to the number of functional groups in a system; functional diversity in an ecosystem is more likely to be high if the number of species is high. Higher functional diversity means the ecosystem will be more stable as well as more robust to any change and external pressures (Bolger, 2001; Emmerson et al., 2001; Giller and O'Donovan, 2002; Kaiser et al., 2005). This subject has been a contentious topic in research as it still remains unclear as to how the decreasing number of species will affect ecosystem function (Tilman et al., 1996; Grime, 1997; Tilman, 1997; Loreau et al., 2001; Giller and O'Donovan 2002; Naeem and Wright, 2003; Hooper et al., 2005; Balvanera et al., 2006; Cardinale et al., 2006; Ieno et al., 2006; Cardinale et al., 2006; Hector and Bagchi, 2007).

Experiments which test the presumed relationship between species diversity and ecosystem function have been largely restricted to terrestrial systems, mainly grassland, but more recently marine systems have also been utilised (Bengtsson, 1998; Loreau et al., 2001). Many hypotheses have been proposed to describe how changes in species diversity may affect ecosystem function. The importance of species diversity to ecosystem function was first coined by Darwin (1859) in his suggestion that a system will be more ecologically stable with the increasing number of species. This theory was extended by MacArthur (1955) who suggested that the stability of the system would increase when the number of trophic groups, along with species diversity, increased (diversity-stability hypothesis - Figure 1.1a). Another theory that relates biodiversity and ecosystem function is described as the rivet hypothesis (Ehrlich and Ehrlich, 1981) (Figure 1.1b). This theory proposed the notion of comparing an ecosystem with a complex structure like an aeroplane with all species in the ecosystem acting like rivets holding the plane together. The total

collapse of the plane is depending upon which, and how many rivets are lost. A few species extinctions do not affect the whole ecosystem function since overlapping function can be compensated by others. Similarly, the third hypothesis (redundancy hypothesis - Figure 1.1c) restates/modifies the rivet hypothesis. This theory suggests that the number of species that are important in maintaining ecosystem processes is limited to a certain threshold. Therefore, additional species above this threshold would not greatly affect ecosystem function. This theory also suggests that species which singularly represent a given functional group should receive most attention in conservation efforts as the loss of these species would have a greater impact on the ecosystem function than a species with a functional group substitute (Walker, 1992). Lawton (1994) proposed the fourth hypothesis (Figure 1.1d), the idiosyncratic hypothesis, where the fundamental principal is that the relationship between species diversity and ecosystem function is very complex. Thus, ecosystem function may be modified when biological diversity changes, but the magnitude and direction of modifications are not predictable due to unpredictability and variation of the role of each species.

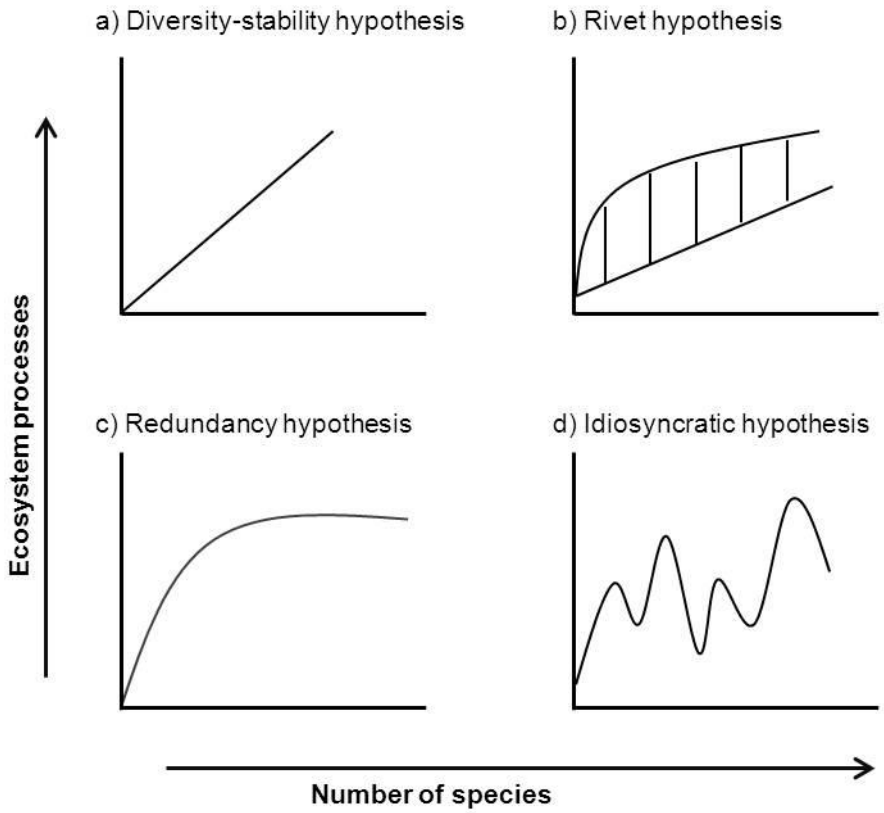

Figure 1.1. Graphical representation to describe the relationship between biodiversity and ecosystem functioning.

The idea of the relationship between biodiversity and ecosystem function has led to an extensive debate which has become one of the central agendas in contemporary ecological research (Loreau et al., 2001; Solan et al., 2009). The emergence of this debate was sparked by the concern regarding the effect on human wellbeing as a result of the reduction in biodiversity and subsequent ecological functioning following anthropogenic changes around the world (Sala et al., 2000; Diaz et al., 2006). There is consensus among many ecologists that biodiversity regulates ecosystem function (Schlapfer and Schmid, 1999), and the relationship between these aspects has been successfully studied under controlled laboratory experiments (Solan et al., 2009). However, those laboratory studies were criticised for being unrealistic (Solan et al., 2009) in terms of its applicability to the real world, and relating the findings to management issues (Srivastava and Vellend, 2005). The disagreement between ecologists also centred on the understanding of the importance of functional substitution and reduction in the number of species that would change the functionality of the ecosystem (Loreau et al., 2001). Nevertheless, studies in the past 15 years have provided evidence for a positive relationship between biodiversity and ecosystem function (Solan et al., 2006; Balvanera et al., 2006; Cardinale et al., 2006). This notion has however received considerable criticism particularly on the basis that, other than the biodiversity, there are many biological and environmental variables that regulate ecosystem function. In terms of biological effect, Bengtsson (1998) argued that diversity has less effect on the ecosystem function compared to the effect imposed by species identity. Furthermore, a relatively recent notion suggests that understanding of the function of the species is more important than the identity of the species itself in understanding ecosystem function (Tilman, 2001; Hooper at al., 2005). This idea concerning functional diversity has the potential to relate the species characteristics (morphological, physiological and phonological) to the ecosystem process (Petchey et al., 2009). The main reason to support this idea is that the functional diversity explains the compensation strategy by one species for the loss of other (Petchey et al., 2009).

Increasing human population, as well as the need for natural resources and space, lead to habitat fragmentation along with habitat destruction and cause species loss (Diaz et al., 2006). Species losses occur locally, nationally and globally, hence this phenomenon will reduce the genetic diversity (Hooper et al., 2005) and ecosystem function (Ehrlich and Mooney, 1983). The consequences of mass species loss to

human activity are potentially huge; including changes in functioning of ecosystems that provide crucial services such as nutrient cycling and photosynthesis. This would have a direct effect on material goods, causing a loss of crops, natural resources, and even medicines. There would also be a loss of non-market values such as the aesthetic beauty of biodiversity. The scientific challenge is to predict the importance of a reduction in biodiversity, to ultimately improve environmental policy in protecting habitats and species richness (Hooper et al., 2005; Fischer and Young, 2007).

1.3.2 Species-specific functional roles

Every species in an ecosystem have a functional role, such as pioneer encrusting suspension feeders (e.g. some polychaetes and bryozoans), competitively dominant encrusting suspension feeders (e.g. some sponges and ascidians), benthic zooplankton feeders (e.g. some anemones), deposit feeders (e.g. echiuran worms), scavengers (e.g. amphipods), mobile carnivores (e.g some echinoderms) and others (Kaiser et al., 2005). Some of the species are classified as being 'keystone' to a community because they have a dominant impact on other species in the ecosystem, thus the loss of these species will impose a greater effect on the ecosystem function and services (Pace et al., 1999).

Many laboratory studies have been conducted to determine the relationship between community composition and ecosystem function in marine benthic systems using several selected species (e.g. Biles et al., 2002; Emmerson et al., 2001; Solan et al., 2008). The results showed that species identity is to some extent important in determining the ecosystem function of the systems. From these studies, it is also equally important to understanding the role of the species in order to be able to predict the effect of changes in community composition on the ecosystem.

Understanding the functional role of species is recognised as being important in order to assess the functioning of ecosystems (Loreau et al., 2001). However, assigning species to specific functional roles has been a real problem to researchers. One has to be very careful to classify species to any functional group where a precise knowledge about the species' biology is needed. This problem can be even greater for habitats with a high number of species where the biological information for many species is limited or not available or. As classifying the species into functional groups is a subjective approach, there is also a possibility that this could be different

between different researchers. Although some efforts have been put into standardising this approach, for example the Biological Traits Information Catalogue (MarLIN), a more thorough coordination is still needed to validate the information for as many species as possible. A further limitation to the functional group approach also related to 'functional plasticity' where some species have a dynamic functional role depending on the time (age and developmental stage) and/or habitat condition (Paterson, 2005).

1.4 Benthic infaunal activity affects sediment stability

Research on sediment dynamics and transport is required to understand and predict (i) morphodynamic and morphological changes, (ii) contaminant distribution in estuarine, coastal and shelf environment, and (iii) interactions between sediment and biota (Collins and Balson, 2007).

Sediment transport will change seabed topography and subsequently has the potential to affect particle deposition (Kenny and Rees, 1996). Dredging activities disturb marine deposits and alter their distribution through releasing sediment into the water body during the dredging operations (Hall, 1994; Newell et al., 1998; van Dalfsen et al., 2000; Boyd et al., 2004; Boyd et al., 2005; Cooper et al., 2005). Local currents will move these sediments away from the dredged area. Thus, if there are any contaminants, they will also be transported to other areas (Newell et al., 1998). However, sediment transport can also promote species diversities as well as moderate the spatial and temporal composition of marine soft sediment communities (Hall, 1994). A severe physical disturbance (e.g. dredging, bottom fishing, and severe storm conditions) can erode the sediment surface to uncover substrata unfavourable to the settlement of organisms' larvae in the area (Kenny and Rees, 1996). Thus, given that sediment transportation for the purpose of coastal management and development is very important, the need to understand sediment stability and movement is increasing (Saunders, 2007).

Most of the studies on sediment stability have been done in intertidal areas with fewer studies in subtidal sediments, since researchers have found it more difficult to work in this area. There are several methods used for determining the sediment stability in both intertidal and subtidal waters (Saunders, 2007). The majority of sediment studies investigating the stability and erodibility of cohesive sediments have been conducted

in laboratory flumes with assumptions that physical and biological characteristics of the sediments remain unchanged during the transport of sediment from field to laboratory (Jumars and Nowell, 1984). The use of laboratory flumes to extrapolate to field conditions is full of compromise and is unsuitable due to the complexity of natural bed sediment (Widdows et al., 1998; Amos et al., 2004). The applications and features of different flumes and instruments for measuring sediment erosion have been reviewed by Black and Paterson (1997).

The annular type of flume has attributes that make it valuable for the study of physical and biological influences on sediment stability and erodibility (both cohesive and non-cohesive). One of the major advantages of the annular flume's design is the constant channel geometry, and infinite flow length resulting in a fully developed boundary layer above the sediment (Amos et al. 1992). Most of the benthic flumes require sediment to be taken to the laboratory, which will possibly disturb the sediment prior to the measurement in the flume. However the use of a box corer makes it possible to collect relatively undisturbed sediment from sub-tidal areas (Jumars, 1975; Green et al., 2002). There are also annular flumes (e.g. Sea Carousel, Mini Flume) which are able to measure the sub-tidal sediment properties *in situ* (Amos et al., 2004). On the other hand, instruments such as the cohesive strength meter (Paterson, 1989) and the submersible shear vane (Hauton and Paterson, 2003) can also be used *in situ* in order to prevent disturbance. The submersible shear vane needs to be operated by a diver and is suited for use in shallow sub-tidal areas.

In terms of their effect on sediment stability, macrofauna can be divided into two main functional groups, namely sediment stabilisers and destabilisers (bio-stabiliser and bio-destabiliser). The categories which describe and relate interactions between macrofauna species and sediment are bioturbation, a process of moving sediment particles vertically or horizontally by organisms (Graf and Rosenberg, 1997; Reise, 2002; Widdows and Brinsley, 2002); tube building, which usually will help to increase sediment stability (Jones and Jago, 1993; Graf and Rosenberg, 1997; Black et al., 2002; Reise, 2002); mucilage production, involving production of mucus trails for the purpose of locomotion which can directly stabilise sediment (Black et al., 2002; Reise, 2002); faecal pellet production, that produces easily eroded sediment material (Minoura and Osaka, 1992); and biodeposition, which may occur when near-bed velocity is reduced by the presence of biological structure (e.g. mussel beds and

macroalgae), or will take place when filter feeding species capture suspended particles and deposit them (as pseudo-faeces) on the bed (Graf and Rosenberg, 1997; Black et al., 2002; Reise, 2002; Widdows and Brinsley, 2002; Kooijman, 2006).

The actions of benthic fauna are not always one dimensional as some organisms are characterised by more than one functional role. The common example in intertidal systems is the polychaete, *Hediste diversicolor*. This worm constructs complex tube galleries to depths of around 15 cm under the sediments (Christensen et al., 2000) and processes the materials in the tubes as their food source, thus making them a deposit feeder. However, the feeding mechanism of *H. diversicolor* can be varied and they can also be a carnivore by feeding on small benthic infauna, act as grazer by feeding on algae (Paterson, 2005), or becoming a filter feeder when their tubes are submerged with water containing suspended particles (Christensen et al., 2000; Paterson, 2005). The ability of this worm to switch from deposit feeding to filter feeding shows the difficulty in predicting the effect of infaunal activities on sediment stability. Certainly, this ability is associated with evolutionary fitness in responding to constant changes in sediment environment which requires organisms to be more flexible to survive.

1.4.1 Sediment stability as an ecosystem function

The processes that take place in an ecosystem will influence and be influenced by various abiotic and biotic factors, making the habitat, the biology and the processes closely interlinked (Saunders 2007). This can be demonstrated by research on sediment systems including aspects of primary production (Forster et al., 2006), nutrient flux (Biles et al., 2002, Biles et al., 2003) and bioturbation (Emmerson et al., 2001; Solan et al., 2004) where any change in the habitat or species composition changes the resulting process (Saunders, 2007).

The overall stability of sediment depends on both biotic and abiotic factors (Jumars and Nowell, 1984; Jones and Jago, 1993). Ecosystem function is a process in an ecosystem involving transport, transfer and metabolism of materials (Chapin et al., 1997; Srivastava and Vellend, 2005). Although materials in that sense referred to chemicals and nutrients, it may be equally applied to the movement of sediment (Saunders, 2007). Hence, stabilising or destabilising influences of an ecosystem on overall sediment stability could be referred to as an ecosystem function (Saunders,

2007). For example, the formation of a bed by mussels may enhance the sediment stability, whilst bioturbation may be a destabilising factor for sediment (Widdows and Brinsley, 2002). There are also activities that can be both stabilising and destabilising factors. For instance, tube building animals may be classified as destabiliser when they build a sparse array of individual tube as this kind of tube could possibly deflect high momentum fluid onto the bed creating scour. On the other hand, animals can be considered as stabiliser when they build a denser array of tubes of which can protect the seabed from a fast and rough flow on it (Jumars and Novel, 1984).

1.5 Marine aggregate dredging in the UK

Aggregate is a collective term for crushed rock, sand and gravel (Gubbay, 2005) that is widely used as raw materials in the construction industry (Boyd et al., 2004; Newell et al.; 2004, Boyd et al.; 2005, Cooper et al.; 2005). Aggregate extraction in the marine area accounts for approximately 21% of the total production in England and Wales (Cooper et al., 2007b; Hill et al., 2011). The landing of aggregate materials from licensed areas around England and Wales is normally more than 20 million tonnes every year (Gubbay, 2005; Hill et al., 2011), which is equivalent to approximately 50 quarries if the same amount was to be collected on land (Hill et al., 2011). The extraction of marine aggregate has provided clear economic gains for the UK and steadily increased until 1989 and has since continued in steady state (Boyd et al., 2004). Although most marine aggregate is used for domestic construction, there is a gradual increase of marine aggregate materials from UK waters being exported to countries such as France, Belgium and the Netherland for the same purpose (DEFRA, 2002). Sometimes, this seabed material is also used for beach nourishment and coastal defence, with around 20 million tonnes used in the 1990s for this purpose (Gubbay, 2005).

In England, a dredging ‘permission’ is granted by the Marine Management Organisation when the predicted impacts of proposed dredging are deemed acceptable. Production licences are subsequently issued by the Crown Estate, the owner of the UK seabed (MMO, 2010). Since 2005, seventy licences in coastal waters around England and Wales have been issued by the Crown Estate for marine aggregate extraction operations (Figure 1.2). The majority of these licenses were allocated for works in the South and East of England, although several of the licenses for dredging works in the Bristol Channel and Irish Sea were also granted (Gubbay,

2005; Hill et al., 2011). There is currently no dredging permitted within Northen Ireland and Scottish waters due to lack of suitable marine resources and also because there is an adequate supply of aggregate from land available in these countries (Tillin et al., 2011).

Figure 1.2.: Locations of current (2010) licenced dredging areas licensed by the Crown Estate (Hill et al., 2011).

The main dredging techniques used today are anchor dredging and trailer dredging. Anchor dredgers usually operate over deep deposits (e.g. Isle of Wight and Bristol

Channel) and only move a few metres (Boyd and Rees, 2003), while trailer dredgers work in relatively shallow deposits by trailing a suction pipe along the seabed at a speed around 1-3 knots (0.51 ms^{-1} to 1.54 ms^{-1}) (Gubbay, 2005). According to Mineral Industry Research Organisation (MIRO) (2004), more than 75% of all aggregates in the UK have been collected using the trailer dredging method (Figure 1.3). Once on site, the trailer dredger lowers one (or more) suction pipes to the seabed, and centrifugal pumps are used to suck up a sediment-water mixture. The dredger moves forward at approximately 2 meters per second, delivering 3 cubic meters per second of aggregate-water mixture to the 30000 cubic meter capacity hopper. It takes approximately 3-6 hours to fill the hopper on site, and this is then discharged at a shore facility (MIRO 2004).

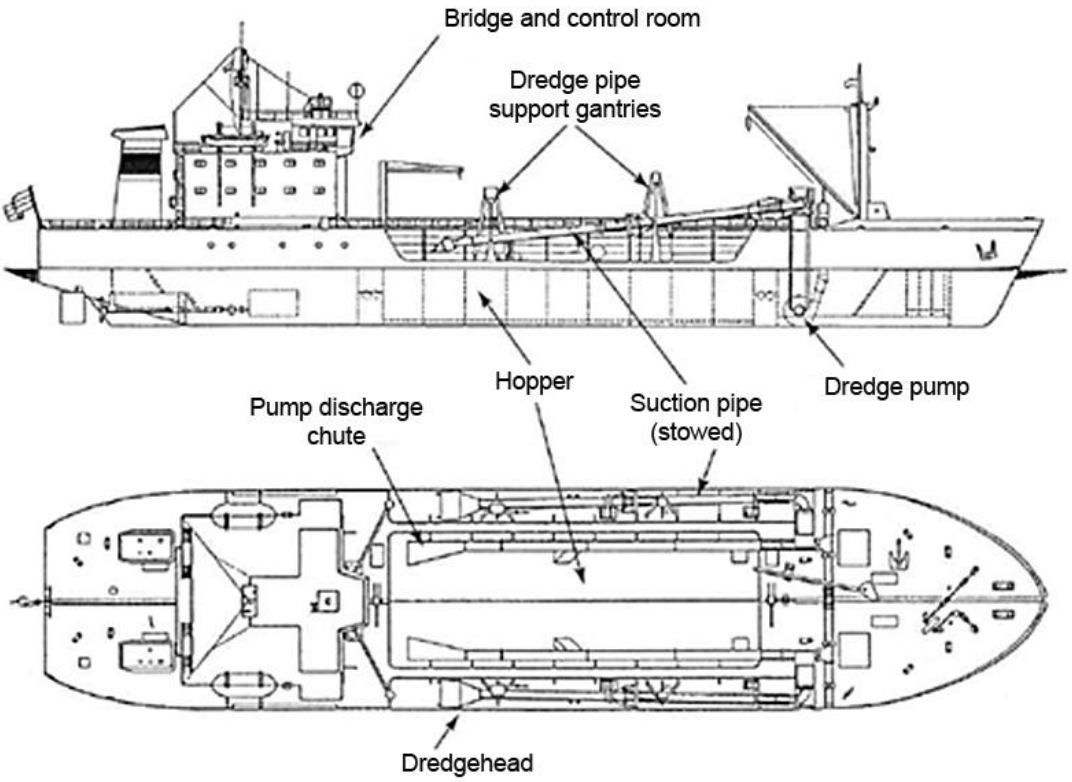

Figure 1.3. Main features of the trailer dredger.

Regulations with strict conditions have been set up by the British government concerning the marine aggregate industry in order to reduce the effect of this activity on the relevant ecosystems. These conditions cover many aspects of the specific site, for instance, the return of the seabed to a 'similar' condition as prior to the dredging, and monitoring of the environmental attributes before, during and after dredging (DEFRA, 2002) are required. Licence conditions also include seasonal

restrictions on dredging, limitations on dredging rate and restrictions on the practice of screening (DCLG, 2002). Screening is the process of returning unwanted particular size fractions of the dredged material at sea in order to obtain a cargo that has an optimum mixture of sediments for customer requirement (Boyd et al., 2003). However, the return of unwanted fractions also causes an adverse impact on the system through the development of a sediment plume (DEFRA, 2002; Smith et al., 2006). There are several licenced areas subjected to screening work, for example Area 222 and Area 408 in southeast England. Meanwhile, all materials dredged from Hastings Area X and Y, in south England are loaded without screening (Boyd et al., 2004; Cooper et al., 2005).

The UK government shows great care in minimising the long-term effects of dredging on the environment, and it has induced a number of initiatives to assess and to determine the recovery of the seabed after dredging work (Cooper et al., 2008). This is important given the fact that aggregate extraction industry supports the UK economy, which is mostly through aggregate sales (Tillin et al., 2011). Moreover, construction activity increases the pressure to obtain aggregates from marine sources (Gubbay, 2005). Other than economic benefits, marine aggregate dredging also produces social benefits through employment and the use of material (mostly sands) for beach replenishment (coastal defence) (Tillin et al., 2011). Considering beaches provide recreational areas and also mitigate the effect of coastal erosion, these features may compensate any initial disturbance caused (Austen et al., 2009).

1.6 Effect of dredging on macrofaunal assemblages and sediment characteristics

Changes to the biological and physical characteristics of an area influenced by dredging operations can be via direct effects; such as through the removal of sediment, the removal of associated biota, the smothering and destruction of biota due to the dredge head and through the influence of the sediment plume on benthic and pelagic organisms. Alternatively, effects may be indirect through sound pollution, and the release of nutrients. These problems often also influence the seabed or water body in areas adjacent to the dredged area (Newell et al., 1998; van Dalfsen et al., 2000; Boyd et al., 2005) and this has to be included when considering the potential environmental influence of dredging. A number of extensive studies have been carried out to determine the effect of marine aggregate dredging on macrofaunal

communities in European waters (e.g. Millner et al., 1977; Pagliai et al., 1985; de Groot, 1986; Sips and Waardenburg, 1989; Kenny and Rees, 1994; Desprez, 2000; Sarda et al., 2000; Boyd et al., 2004; Newell et al., 2004; Sánchez-Moyano et al., 2004; Szymelfenig et al., 2006; Simonini et al., 2007; Cooper et al. 2008; Hill et al., 2011; Tillin et al., 2011). The common biological effects associated with dredging including the reduction of number of species, individuals and diversity of communities. Meanwhile the physical impact of dredging can be the formation of a sediment plume; when materials are discharged into the sea through an overspill chute or through the screening process (Kenny and Rees 1996; Newell et al., 1998; van Dalfsen et al., 2000; Van Dalfsen and Essink, 2001; Boyd et al., 2003; Boyd et al., 2005; Cooper et al., 2007a; Cooper et al., 2007b).

The effects of dredging are not always confined to dredging area, but have been observed in the surrounding areas (Boyd and Rees, 2003; Newell et al., 2004; Robinson et al., 2005; Cooper et al., 2007). For example, the increase of abundance and biomass of macrobenthic species in neighbouring areas after the dredging works (Poiner and Kennedy, 1984; Newell et al., 2004). This phenomenon might be due to organic enrichment derived from fragments of the marine benthos that are initially extracted from the sediment but then are returned together with the outwash water (Newell et al., 1999). Changes to the composition of the macrofauna of the dredge site are most likely due to the difference in sediment size created by the dredging activity (Boyd et al., 2004; Szymelfenig et al., 2006). However, there are also some areas where changes in sediment composition have less significant impact on macrofaunal community (Cooper et al., 2011).

1.6.1 Recovery of macrofauna following dredging works

The effect of marine aggregate dredging on the natural function of the seabed and associated benthic fauna has been widely studied (e.g. Poiner and Kennedy, 1984; Van der Veer et al., 1985; Newell et al., 1998; Boyd et al., 2003; Boyd et al., 2004; Cooper et al., 2005; Robinson et al., 2005). However, studies of the effect of long-term dredging on the recovery of fauna are still scarce (Boyd et al., 2003; Boyd et al., 2004; Cooper et al., 2007b). Understanding the recovery of macrofauna following dredging activities is very important as it helps to provide information on the best way to control dredging and rehabilitate the dredged areas after disturbance (Boyd et al., 2004).

A degraded ecosystem is often considered to achieve recovery once it returns to original (before disturbed) condition (Elliott et al., 2007). However, recovery can be considered in a number of different ways. For example, ecosystem recovery can be evaluated to examine how fundamental ecological processes, community function and various ecosystem services are affected (Elliott et al., 2007). However, the important issue that needs to be considered is whether the ecosystem can ever return to, and be sustained in its original condition (Simenstad et al., 2006). Since this may be difficult to achieve (Borja et al., 2010), indicators based on structural, functional and socio-economics could provide a sensible way of assessing recovery (Elliott et al., 2007). Furthermore, as defined in some legislation such as the Water Framework Directive and the Marine Strategy Framework Directive in Europe, and the Clean Water Act, in the USA, one of the primary goals in ecosystem management is to restore the degraded habitat (Apitz et al., 2006; Borja et al., 2008).

There are two main types of recovery, namely passive and active recovery. Passive recovery will begin once stressors have been removed from a system (e.g. disturbance stopped). This type of recovery depends on the ability of the system to redress damage due to any change or to attain an improved structure and functioning based on several properties (Elliott et al., 2007). These properties are: 1) recoverability, which is the ability of a system to return to a state which is near the condition before disturbance occur (Tyler-Walters et al., 2001); 2) resilience, which is defined as 'the ability of an ecosystem to return to its original state after being disturbed (Elliott et al., 2007); 3) adaptation, which is a strategy used by communities to increase their resilience (Elliott et al., 2007); 4) carrying capacity, which is the maximum population size that a system can accommodate (Elliott et al., 2007). In contrast, active recovery is a process where human intervention is used to improve the damaged habitat. Such intervention could include: 1) restoration, where the habitat is altered in order to return to its pre-existing state (Simenstad et al., 2006); and 2) re-establishment, where a species (especially a structuring species) is reintroduced to the damaged area (where it has disappeared) in order to restore the ecosystem function (Elliott et al., 2007). Examples of active recovery including restoring the seabed surface after dredging by means of gravel seeding (Cooper et al., 2011) and the use of shell material (Collins and Mallinson, 2006) to promote faunal recovery and reintroducing corals and other biogenic reefs through

transplantation in order to re-establish this habitat (Elliott et al., 2007). In addition, active recovery also refers to the response to a single stressor. The response could be through 1) mitigation, which is the act to reduce the damage suffered by the habitat; and 2) habitat enhancement, which is an act to increase the ecological value of the habitat (Elliott et al., 2007). Collectively, recovery is defined as all aspects that support the improvement and restructuring of the damaged habitat, recovering its use and restoring its biological potential (Elliott et al., 2007). Nevertheless, recovery is not a straight forward concept to be applied to faunal communities due to their complex composition and consistently changing structure over time, even in undisturbed areas (Newell et al., 1998).

The recovery process of benthic assemblages in dredged seabed areas is normally linked to changes, in terms of grain size, organic content and seabed structure as affected by the sand extraction (Simonini et al., 2007). In addition, recovery also depends on hydrodynamic regime, water mass transport, size and depth of the area, dredging methods and duration of aggregate extraction, degree of ecosystem disturbance, and biological features of neighbouring areas (Newell et al., 1998).

A number of studies have investigated physical and biological recovery after dredging and since there are many factors shaping the community in the dredged and adjacent areas, it is not surprising to find that rate of recovery proposed in different studies is highly variable (Newell et al., 1998). A number of researchers found that the recovery of benthic communities may be completed within a range of 2 to 4 years after dredging ceased (Sarda et al., 2000; van Dalfsen et al., 2000; van Dalfsen and Essink, 2001). However, Boyd et al.; (2005) and Cooper et al., (2007b) found this time to be too short, and they suggest a more suitable recovery period of 9 and 7 years, respectively. Rapid recovery is normally associated with areas dominated by mobile opportunistic species. The characteristics of these species with rapid reproduction and growth rates help to promote a faster recolonisation of the fauna after disturbance. Contrary to this, a longer recovery rate is commonly recorded in areas with higher numbers of long-lived and slow-growing species. These species normally need several years for the recruitment of larva and subsequent growth of the juveniles (Newell et al., 1998). Apart from the biological factors, the sediment types also affect the recovery rate of macrofaunal community. Recovery in the habitat characterised by fine-grained deposits such as muds and clays normally takes up to

1 year (Ellis et al., 1995) or between 1 – 3 years in the case of coastal ecosystems such as Waddensea in the Netherlands (van der Veer et al., 1985). A longer period is apparently needed for the communities inhabiting sand and gravel deposits to recover (Kenny and Rees, 1996).

1.7 The present study

The first part of the thesis concerns a field investigation of the impacts of aggregate dredging on the benthic community and ecosystem function in Area 222. Marine aggregate dredging is known to directly disturb and change the characteristics of the seabed. This disturbance will inevitably change the nature of the site specific assemblages of macrofauna. However, the way and the degree to which this operation can affect the benthic ecosystem and its functionality still remain ambiguous. Hence, the aim of this study was to determine a suitable recovery period for macrofaunal assemblages and perhaps more importantly, the related ecosystem functions. The ecosystem function was measured based on comparison between dredged and undisturbed area over a period from 2001 to 2007 (no data was recorded in 2005 and 2006). This information could therefore be used by regulators, conservation agencies and the marine aggregate extraction industry to decide the best way to minimise the environmental footprint of dredging, as well as to create a more balanced debate about the acceptability of disturbance following dredging operations. The second part of the thesis was a laboratory experiment to determine the effect of benthic fauna and its body size on sediment stability. A more detailed description of the present study is presented as follows:

Chapter 3: Ecosystem function following marine aggregate dredging was investigated using traditional statistical analysis. Common indices such as abundance, biomass, species diversity and taxonomic diversity were used to quantify the recovery rates of macrofaunal community after dredging ceased.

Chapter 4: Recognising that every species has its own function in an ecosystem and the loss of one species will not necessarily change the ecosystem function, the measurement of ecosystem function in this chapter was based on a more novel approach using functional traits analysis. Five techniques were employed: the Infaunal Trophic Index (ITI), Somatic Production (Ps), Biological Traits Analysis (BTA), Rao's Quadratic Entropy coefficient (Rao's Q) and Functional Diversity (FD).

Chapter 5: Assessment of the dredging impact on sediment characteristics is presented. The impact was expressed by changes in sediment structure. This is more relevant given the fact that Area 222 is a shallow (27 – 35 m) coastal area, hence the seabed habitat of this area is more prone to disturbance compared to the habitat in deeper water. In addition, this chapter also explains the effect of changes in sediment distribution on macrofaunal assemblage and ecosystem function.

Chapter 6: Although measurement based on functional traits is deemed a powerful tool in quantifying ecosystem function, assigning every species to functional groups can be problematic and time consuming. More importantly, there are many different indices based on this approach proposed by many authors and that makes it complicated for environmental managers and policy makers to decide which the best and most suitable index is. Realising this issue, a more general and simpler approach is presented where the species were assigned to two most relevant functional roles, namely feeding mechanisms and mobility. Using this approach, the relative proportion of different functional groups following disturbance was determined. In addition, the influence of particle sizes on the distribution of these groups was also investigated.

Chapter 7: Finally, a general discussion of the results and their implications is presented.

Main thesis questions to be addressed

1. While the recovery of macrofaunal communities at the low dredging intensity site has already been observed (based on several traditional indices), the main question is to determine whether such recovery has occurred at the high intensity site within the study period *(Chapter 3).*

Hypothesis: Based on predictions from previous studies, the recovery at the high intensity site takes place in 2007.

2. Determine the difference in recovery times based on both traditional and functional analyses (Chapter 3 and 4).

Hypothesis: Recovery based on functional analysis is faster than recovery based on the use of traditional analyses.

3. Identify any relationship between sediment particle size and the biological recovery based on both traditional and functional analyses (Chapter 5).
Hypothesis: Gravel deposits provide a stable habitat for the macrofauna, and therefore have a close association with faunal recovery.

4. Identify if there is any trend in the faunal recovery in terms of the main functional groups (Chapter 6).
Hypothesis: The return of gravel deposits creates a favourable habitat for the recovery of sessile filter feeders.

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Chapter 2: General methods

This chapter describes the methods used in the study of the impact of dredging on macrofaunal communities (Chapters: 3, 4, 5 and 6). All field work (2001 – 2004 and 2007) was conducted by the Centre of Environment, Fisheries and Aquaculture Science (CEFAS). Sample processing (both biota and particle size) and macrofaunal identification for the datasets from 2001 – 2004 were completed by CEFAS. Meanwhile, sample processing and identification of the new dataset (2007) were carried out by the author.

2.1 Study area

Area 222 (Figure 2.1) is located approximately 20 miles to the east of Felixstowe, off the southwest coast of England. The depth of the water ranges from 27 m and 35 m against the Lowest Astronomical Tide (LAT). The first licensed dredging in this area was carried out in 1971 with approximately 0.3 km^2 of extraction area. Dredging activity reached its peak in 1974 with 872,000 tonnes of aggregate removed per annum and ceased in 1997. There is limited information on the dredging methods; however it is believed that the materials from this area were extracted using trailer and static suction hopper dredging (Boyd et al., 2004). In addition, a screening process was also believed to have taken place in order to alter the sand:gravel ratios as required by customers. A recent study by Cooper et al. (2005) covering the period from 2001 to 2004 found that the macrofauna of the area was dominated by a number of polychaete worms (e.g. *Pomatoceros lamarcki, Lanice conchilega and Lumbrineris gracilis*), Crustacea (*Pisida longicornis)*, echinoderms (*Amphipholis squamata* and *Echinocyamus pusillus)*; and also a high abundance of colonial species such as hydroids (*Sertularia cupressina*, *Plumularia setacea*,) and bryozoa (*Alcyonidium mytili* and *Bugula plumosa)*.

The geology of the area is characterised by an eroded basal unit of London Clay which is overlain by Pleistocene sediment deposited during the drainage of the land surface that existed at the end of the Pleistocene. These sediments were re-worked during the Holocene to form thin (generally <1m) veneers of gravelly sediments. Thicker deposits of these sediments are present within paleovalleys (Harrison, 1998). The thickened section of the sediments appeared to be the area where high concentrations of dredging activity have taken place (Boyd et al., 2004). There were

different intensities of dredging in the licensed area itself where at its highest activity was up to 39.5 hours in 100 m by 100 m box, or at the lowest, less than 1 hour. The differences in intensity were used to determine the high and low dredging intensity sites for sample collections (see section 2.2) (Boyd et al. 2004, Cooper et al. 2005).

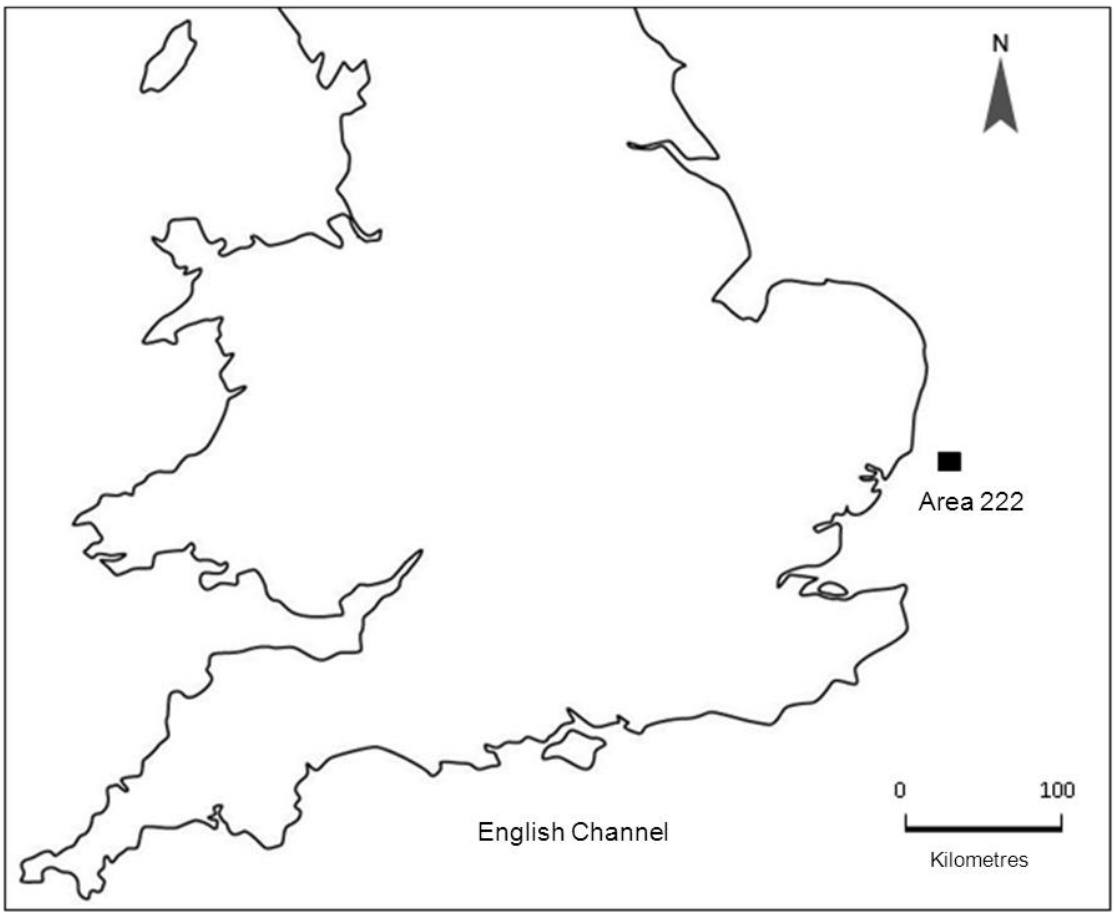

Figure. 2.1. Location of Area 222, the main study area.

Boyd et al. (2004) reported that the eastern side of dredging area were predominantly sandy-gravels with little fine materials (silt/clay) present (Figure 2.2). Similar sediment characteristics were recorded within the dredging area itself. The predominant sandy-gravel sediments were distributed in the shallow plateau to the east of this area. The proportion of finer sediments increased in the western side of the area. These sediments were recorded mainly in the deep water channel feature of the western part of Area 222. Sediments within the dredging boundary also show a distinct separation depending on the intensity of the dredging. The lower dredging intensity site was characterised by coarse particles with a high proportion of gravel, while

higher dredging intensity site comprised a higher proportion of medium sand (Cooper et al., 2005).

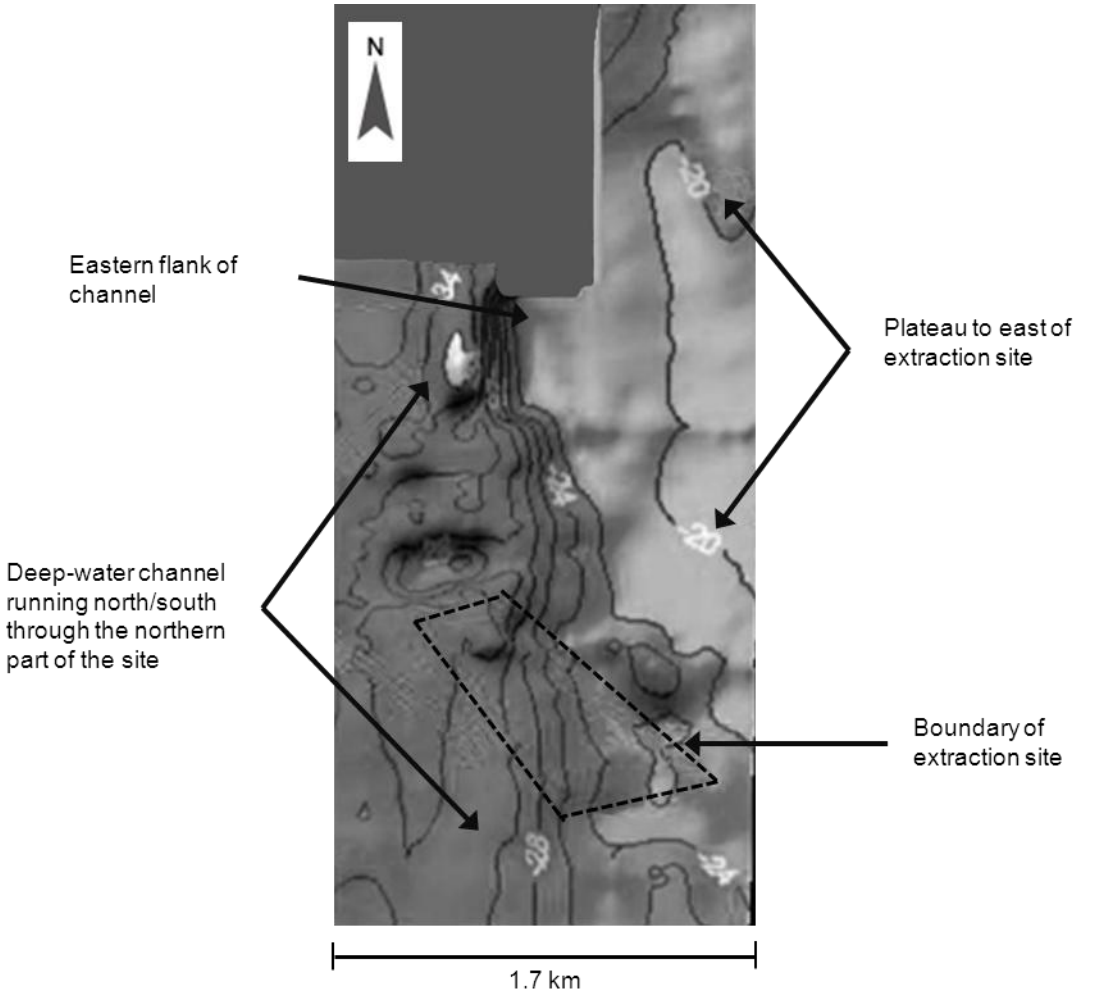

Fig. 2.2. Three dimensional contoured plots derived from the single line bathymetric survey carried out in 2001 at Area 222. Figure adapted from Boyd et al. (2004).

2.2 Field samplings and measurements

Since 1993, an Electronic Monitoring System (EMS) has been fitted to all dredging vessels on a Crown Estate licence (Boyd et al., 2004; Cooper et al., 2005). Information obtained from EMS was used in order to determine the dredging intensity of different sample areas. The selected sampling sites (Figure 2.3) were separated into high dredging intensity (High: > 10 hours of dredging within a 100 m by 100 m block during 1995), low dredging intensity (Low: < 1 hour of dredging within a 100 m by 100 m block during 1995), and two undisturbed (referred to as Reference) sites (Boyd et al., 2004; Cooper et al., 2005). All sampling works were carried out from

2001-2002 using research vessel RV Cirolana and from 2003-2004 and 2007 using RV Cefas Endeavour. In order to avoid any significant seasonal effects, all fieldworks were undertaken at the same time of year, between May and July.

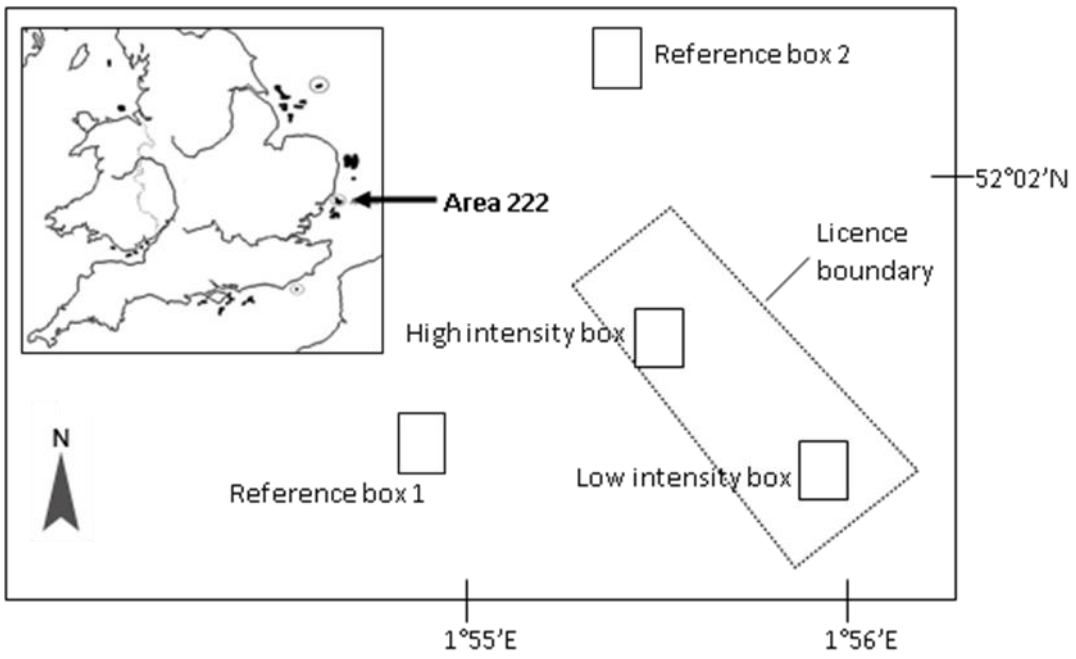

Figure 2.3 Locations of licensed dredging and undisturbed reference sites.

2.3 Sample collection and storage

Samples for macrofaunal assemblages and sediment particle size distributions were collected using a 0.1 m^2 Hamon Grab (Figure 2.4). This device is considered as one of the most effective for course substrata (Kenny and Rees, 1996; Seiderer and Newell, 1999). Ten replicate samples were randomly taken within high and low dredging intensity sites, and 5 replicate samples were collected at both reference sites, totalling 30 samples per year. Once the grab samples were taken on-board, a 500 ml sub-sample was removed from the grab and transferred into a small container and stored in a freezer for particle size analysis (in the laboratory). The remaining sample was then washed over 5 mm and 1 mm square mesh sieves with seawater to remove the fine sediment. The sediment remains on both screens was then back-washed into separate labelled containers and fixed in 4-6% buffered Formaldehyde solution (diluted in seawater).

Figure 2.4: A Hamon grab used in sediment collections for every sampling. This device samples an area of 0.1 m^2 and penetrates up to 15 cm into the sediment (DTLR, 2002).

2.4 Macrofaunal sample processing and identification

Guidelines by DTLR (2002) were used as reference for macrofaunal sample processing. The > 5 mm samples were washed with fresh water over a 1 mm screen in a fume cupboard to remove the formaldehyde solution. The samples were then back-washed into a 10 litre bucket and filled with fresh water. Separation of smaller and lighter animals from sediments was done by gently stirring the sample until the animals were suspended, before being decanted over a 1 mm mesh screen. A small portion of sediment was then placed onto a plastic tray (Figure 2.5) and examined under an illuminated magnifier to check for any remaining animals (such as molluscs and echinoderms) that had not been recovered in the decanting process. This process was repeated until there were no more animals remaining in the sediment. All specimens were then removed into labelled glass vials containing preservative (70% Industrial Methylated Spirit, IMS). Specimens were identified to the lowest possible taxonomic level and counted for every individual. Colonial species were recorded as presence/absence. A collection of samples representing every species found was sent to external contractor (Unicomarine Ltd) for taxonomic verification. For biomass measurements, each taxon in every sample was blotted on absorbent paper before being weighed (wet weight) to the nearest 0.0001 g. The measured wet

weight was converted to ash free dry weights (AFDW) using standard conversion factors (Ricciardi and Bourget, 1998).

Figure 2.5: Samples were examined under an illuminated magnifier to remove remaining fauna.

2.5 Particle size analysis

2.5.1 Wet sieving

Sediment samples were wet sieved using a 500 µm sieve placed on an automated sieve shaker. After 10 minutes, the finer fraction (< 500 µm) was washed through the sieve into a collecting pan, while the coarser fraction (> 500 µm) remained on screen. The wet sieving process was repeated for 3-5 times to ensure all of the finer particles were processed through the sieve. The finer fraction was then transferred into a bucket and left for 48 hours to allow the particles to settle to the bottom of the bucket. A vacuum pump was then used to remove the supernatant after 2 days. The remaining particles were washed into a small container, making sure that the amount of water transferred was minimal. The sample was then left in a freezer at -10°C for 12 hours before being freeze dried at a temperature of between -40°C to -60°C for up to 5 days. The total weight of freeze-dried sample was recorded. Meanwhile, the coarser fraction was washed from the test sieve, and then transferred into a foil tray and oven dried at ~90ºC for 24 h.

2.5.2 Dry sieving

The oven-dried > 500 µm fraction was left to cool to room temperature before being dry-sieved. This step was carried out using automatic shaker containing a stack of sieves of 63 mm to 500 µm (at 0.5 φ intervals) and a collecting pan at the bottom stack. The sieves were placed on a double gyratory motor for a minimum of 10 minutes. The sediments retained on each sieve were weighed to 0.01 g and the values were recorded.

2.5.3 Laser sizing

After the freeze-drying process, the <500 µm fraction was analysed using a laser sizer (Figure 2.6). Prior to that, a sub-sample of ~ 1.5 g was placed into a beaker and 40 ml of 0.1% sodium hexametaphosphate was added. The beaker was then placed in an ultrasonic bath and sonicated for 10 minutes to ensure the entire sample was mobilised. A sub-sample was taken from the beaker using a pipette and then dropped into the laser sizer vessel for analysis. The results were obtained from a PC running Coulter LS 130 software.

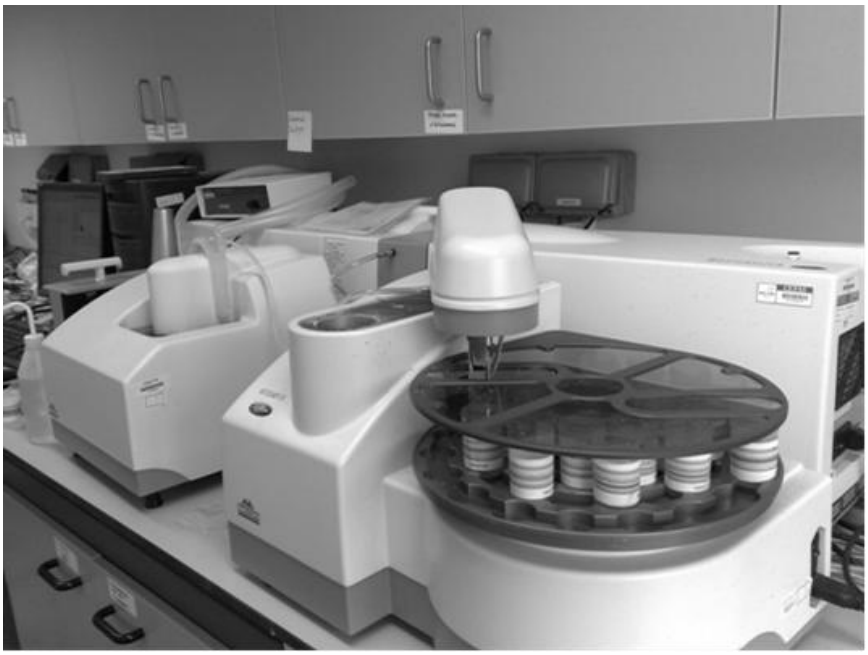

Figure 2.6. Coulter LS 130 laser sizer. This equipment measures diameters of the particles using diffraction technology.

The data from the dry sieving and laser sizing were combined to produce a complete data set of sediment distribution. The composition of the sediment was described

based on Wentworth scale (Bale and Kenny, 2005). Methods used in the particle size analysis were based on the guidelines by DTLR (2002).

2.6 Data analysis

The dataset from 2001-2004 was available from Boyd et al. (2004) and Cooper et al. (2005). The analyses were carried out by combining these datasets with the 2007 dataset analysed by the author.

2.6.1 Traditional statistical analyses

A variety of traditional analyses were used to assess the recovery of macrofaunal assemblages after dredging. These analyses were the species richness (S), abundance (N), biomass (B) (based on Ash Free Dry Weight (AFDW)), Margalef's diversity index (Dm), Simpson's diversity index (Ds) and Taxonomic Distinctness (TD). Further description of the selected indices can be found in Chapter 3. An analysis of variance (ANOVA) test was applied (after assessing that the assumptions of ANOVA were met) using the mean values for each of the above indices to verify the significant difference between different sampling stations and years.

2.6.2 Functional analyses

Cooper et al. (2008) reviewed 12 functional analyses to quantify functional diversity and recommended 5 techniques as being suitable for use with benthic macrofaunal data which was collected from the Hastings Shingle Bank. The selected techniques were Infaunal Trophic Index (ITI), Somatic Production (P_s), Biological Traits Analysis (BTA), and Rao's Quadratic Entropy coefficient (Rao's Q), and Taxonomic Distinctness (TD). Due to the similar nature of the seabed characteristic between these studies, the same indices were selected to be used in the present study with some slight modifications where TD was classified as a traditional index. In addition, another recent index, Functional Diversity (FD), was also selected. Each of the selected techniques is thoroughly described in Chapter 4.

2.6.3 Multivariate analyses

A multivariate statistical approach was used to examine temporal and spatial variation in macrofaunal assemblages and sediment distribution. A similarity matrix of the biological data (e.g. abundance, species richness and the values of functional indices) was constructed using the Bray-Curtis similarity measure. Non-metric multi-

dimensional scaling (MDS) ordination was applied to the similarity matrix to produce a two-dimensional ordination plot representing the similarity between samples/plots. The distance between samples indicates the relative similarity of the multivariate data where samples that are clustered together are more similar than samples that are far apart. Occasionally, the similarity between samples, based on biological data, was presented using cluster analysis. This analysis produces a dendrogram that clusters the samples according to their similarity, such that samples that are clustered into the same branch are more similar than samples that are clustered within other branches. Analysis of similarity (ANOSIM) was performed to test the null hypothesis (H_0) that there was no significant difference between samples collected from different stations. This test produces a value (R value) ranging from -1 to 1; where the value close to 0 indicates the high similarity between samples while the value closer to 1 indicates that the samples are becoming less similar. In unusual cases, where the similarity between samples is higher than the similarity within samples, the ANOSIM test produces a negative R-value. The nature of the community groupings identified in the MDS ordinations was further explored by applying the similarity percentages program (SIMPER) to determine the contribution of individual species to the average of dissimilarity between samples. In contrast to the MDS that was used for biological data, a principle component analysis (PCA), based on Euclidean distance was applied to sediment distribution data to identify any group of samples with similar sediment characteristics. The correlation between macrofaunal assemblages and environmental variables was analysed using Bio-Env routine. This technique was used to investigate if the same groups of species or the same functional traits have any relation with the size of the sediments. This is done by produce a rank correlation of two similarity matrices (biotic and environmental) to determine which sediment particle attributes that best explains the distribution pattern of macrofaunal community. The Bio-Env procedure was also applied to functional groups data (Chapter 6) to determine which set of functional groups best explains the observed macrofaunal community. All multivariate analyses were carried out using PRIMER (Plymouth Routines In Multivariate Analysis of Variance) package version 6 (Clarke and Gorley, 2006).

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Chapter 3: Changes in community structure of benthic macrofauna following marine aggregate dredging

3.1 Introduction

Traditional statistical analyses to assess biological recovery have been based on the re-establishment of a faunal assemblage similar to the community that existed prior to the disturbance; or by means of a comparison between altered areas and natural undisturbed reference areas (Cooper et al., 2007). Several indices, such as number of individuals, number of species and biomass, have been used to assess the status of community assemblages following aggregate dredging (Kenny and Rees, 1996; Carvalho et al., 2001; Boyd and Rees, 2003; Newell et al., 2004; Sanchez-Moyano et al., 2004; Cooper et al. 2005). According to Gray (2000), the number of species alone does not represent the real structure of an assemblage in a community because the number of individuals per species varies. Most popular indices use a combination of species richness and evenness, for example the Margalef index and the Simpson index (Magurran, 2004).

The diversity indices discussed provide a measure of alpha diversity, which is a measurement that describes the diversity within a particular area or community (Magurran, 2004). In contrast, beta diversity (Whittaker, 1960) is a diversity measurement for comparing species composition among different sites or along environmental gradients. Beta diversity reflects the changes in assemblages with species being added, removed or replaced. Whittaker (1960) originally suggested that Beta diversity is for assessing diversity between samples across environmental gradients, but Magurran (2004) argued that applying this index on different spatial and temporal configurations is also valid. The changes in diversity along these configurations are referred to as ‘turnover’ (Maguran, 2004). Beta diversity is an important concept of understanding ecosystem function, for ecosystem management and for conservation of biodiversity (Legendre et al., 2005). In relation to dredging work, beta diversity is deemed appropriate to measure the difference between the dredged and undisturbed sites, and how faunal communities can change over the period of recovery.

Although the alpha and beta diversity measures are useful in assessing the community structure, these techniques treat the species or taxa as equivalent entities (i.e. they don't discriminate between taxa). This is potentially problematic as different species perform various different functions in ecosystems. Intuitively, a faunal community in which a function is provided by only one taxon is considered less diverse than where that same function is provided by different taxa. Thus, the use of taxonomic diversity which incorporates the phylogenetic information is important in assessment of the ecosystem function.

Previous work by Cooper et al. (2005) has been carried out in the Area 222 to determine the recovery of macrofaunal community after cessation of dredging. The study was carried out from 2001 to 2004, and the assessment was based on three indices namely abundance, biomass and species richness. Their study found some evidence of recovery at the site subjected to low dredging intensity 7 years after cessation of dredging. In contrast, no recovery was observed at the site with a higher dredging intensity. Therefore, the present study was carried out to explore the trend of recovery at the low intensity site since 2004, and at the same time to determine if the high intensity site had recovered 11 years after dredging ceased. Similarly, this was done by assessing the benthic community structure at dredged sites and comparing with the natural undisturbed sites. This study also determined how different dredging intensity leads to different recovery times. Several different indices that were based on different theoretical foundations (see Methods section below) but previously unused at this site were also applied in the present study. By providing data for a longer period, this study will make a useful contribution to the dredging industry and its regulators in terms of increasing understanding regarding the rate of recovery, as well as the natural variability of macrofaunal communities in gravelly deposits. The natural variability of the community is a very important aspect especially in the case of this study where the assessment of recovery was by means of comparing the impacted and reference sites. A better understanding of natural variability will avoid the misinterpretation of the recovery trajectory. Also, the use of additional indices may provide a better understanding of recovery. However, it is acknowledged that here may be some discrepancy in interpretation of recovery depending on the vested interests of the group.

3.2 Methods

3.2.1 Measurement indices

All indices were calculated and plotted for each site over time in order to identify any trends in community composition. Abundance (N) and species richness (S) were simply the mean number of individuals and number of species recorded. Biomass (B) was calculated using standard conversion factors (Ricciardi and Bourget, 1998) and expressed as Ash Free Dry Weight (AFDW). In addition to classifying the fauna into species (at the lowest possible taxonomic level), classification was also carried out to major taxonomic groups for a general assessment. These groups were Polychaeta, Crustacea, Mollusca, and Echinodermata, while other small groups were classified as 'Others'.

Rarefaction was used to re-calculate the number of species based on an equal sample size (i.e. species richness drawn from the same number of individuals). The sample-based rarefaction was calculated by repeated re-sampling, using *EstimateS* which is freely available (Colwell, 2006).

Besides species richness, the other diversity indices used in the present study were the Margalef index (Dm) and the Simpson index (Ds). Margalef index was calculated by dividing the total number of species S, by the total number of individuals, N, in the sample (Magurran, 2004):

$$\mathrm{Dm} = \frac{(S-1)}{\ln N}$$

Simpson index (Ds), was calculated based on the probability that if any two individuals are randomly picked from a large community, they are likely to be of the same species. This index is expressed as:

$$\mathrm{D} = \sum\left(\frac{n_i[n_i-1]}{N[N-1]}\right)$$

where, *ni* is the number of individuals in the *ith* species; and *N* is the total number of individuals. The original Simpson index increases as diversity decreases. For an easier interpretation, Ds in the present study is expressed as 1 – D with the range of index value is from 0 to 1 (1 is maximum diversity) (Magurran, 2004).

Calculation of species turnover from site to site and from year to year was based on Beta diversity (β-diversity). The index used in this study, Whittaker index (Whittaker, 1960) is one of the simplest yet most effective (Magurran, 2004). This is expressed as:

$\beta w = S / \alpha$

where, S = the total number of species recorded between two samples; and α = the average number of species from the two samples. The values of the Whittaker index range from 1 to 2, where 2 is maximum diversity (no overlap in species composition). In order to standardise the scale with other diversity indices used in this study, the Whittaker index was expressed as βw-1 to produce a range from 0 to 1, where 1 is maximum diversity.

Diversity of the communities based on taxonomic difference was calculated using Taxonomic Distinctness (TD). TD measures the average taxonomic distance, which is the path length between two randomly chosen species, traced through the taxonomic classification in an assemblage. The TD value is obtained through a simple calculation; by dividing the path length of every pair of species in the list by the total number of paths. This information is arranged in a species-by-sample data matrix with corresponding taxonomic classification for calculation using the PRIMER 6 package (Clarke and Warwick, 2001). The use of only presence/absence data make TD less affected by variations in sampling effort or incomplete sampling (Clarke and Warwick, 2001; Magurran, 2004).

Multivariate analysis to measure the similarity/dissimilarity between sites was based on non-metric multidimensional scaling (MDS), and was confirmed by the R value of ANOSIM. SIMPER analysis was applied to quantify the taxa which contributed the most to the similarity between samples (see chapter 2). Other than the MDS, the similarity between samples was also presented on a dendrogram from cluster analysis.

Where recovery was judged to be incomplete in 2007 (at the high intensity site), best fit lines were fitted to the data in order to predict the likely time required for recovery. The prediction was made by fitting the best fit line (linear and exponential) to the sample data (indices values). These lines were compared to the linear line of the average value at the reference sites to determine the number of years needed by the

macrofaunal community to fully recover (i.e. achieve a value similar to the reference sites). This prediction was made based on abundance, biomass, species richness and Margalef index.

3.3 Results

Overall, a total of 27,768 individuals from 366 taxa were encountered at Area 222 from the 150 samples collected in this study from 2001-2007. In addition, 64 colonial species were also encountered. The macrofaunal abundance was dominated by Polychaeta (37 families), followed by Crustacea (52 families), Mollusca (38 families), Echinodermata (11 families) and others (17 families).

3.3.1 Abundance and biomass

Abundance and biomass showed clear differences between sites over the period of the study (Table 3.1). Lowest values of both measures were consistently found at the high dredging intensity site. In contrast, highest values of both abundance and biomass, were found at the low intensity and reference sites. The high intensity site accounted for only ~10% of both the overall abundance (2891 individuals) and biomass (5.16 g) encountered in this study. The low intensity site recorded the highest abundance with 13,753 individuals (50% of the total abundance), while the highest biomass was encountered at the reference site with 25.33 g (51% of the total biomass).

Table 3.1. Total number of individuals (N) and biomass (AFDW, g) recorded at each sites during the study period.

	Site	2001	2002	2003	2004	2007	Total
Abundance	High	338	410	297	725	1121	2891
	Low	1424	2121	2491	5151	2566	13753
	Ref	2709	2619	1917	2212	1667	11124
Biomass	High	0.79	0.31	1.19	2.08	0.79	5.16
	Low	3.72	3.07	2.63	6.66	3.11	19.19
	Ref	8.39	2.76	7.27	3.65	3.26	25.33

A summary of mean values for the number of individuals and biomass at each site during the study period is given (Figure 3.1.). The undisturbed reference site recorded no significant variation of both abundance and biomass over time (one-way ANOVA, $p > 0.05$). The abundance was significantly lower ($p < 0.05$) at the high intensity site than the reference site from 2001 to 2004, but by 2007 the difference

was not significant ($p > 0.05$) (Figure 3.1a). In contrast to the reference site, the low intensity site recorded a significant variability ($p < 0.05$) in 2004 where the abundance was the highest. As with abundance, biomass at the site of high dredging intensity was also consistently lower than either the low intensity or reference sites (Figure 3.1b). A significant difference between the high dredging intensity and reference sites was recorded in 2002 and 2007 ($p < 0.05$). Meanwhile, there was no significant difference in biomass between the low intensity and reference sites, although in most years biomass at the low intensity site was lower than at the reference site, with the exception of 2004. The higher than expected values in 2004 for both abundance and biomass at the low intensity site was due to the exceptionally high abundance of *Pomatoceros lamarcki*. Together with other species including *Pisidia longicornis*, *Lumbrineris gracilis* and *Amphipholis squamata*, *P. lamarcki* also contributed to the dissimilarity between the high intensity site and the other sites.

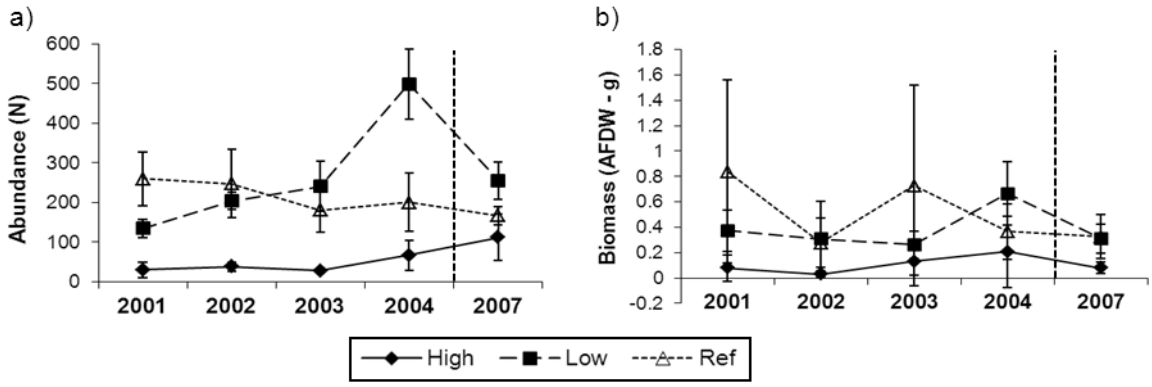

Figure 3.1. Summary of means and 95% confidence intervals of a) number of individuals and b) biomass (AFDW) at sites of the high and low dredging intensity sites and reference site. The dotted vertical line indicates the discrepancy in time intervals.

Similarly, Multidimensional Scaling (MDS) ordinations of samples, based on abundance and biomass data display a fairly identical distribution (Figures 3.2 and 3.3). Overall, the wider separation of samples from the high intensity dredging and reference sites implies a lower degree of similarity than is evident between the low intensity and reference sites. Overall, the site with high dredging intensity demonstrates a greater discrepancy from the reference sites, however the temporal data show these sites becoming more similar particularly in 2007 as evident from the closer samples between these sites. The tendency towards increasing similarity between the high intensity and reference sites is confirmed by a decline in R-values from an ANOSIM test for 2007 (Table 3.2). The low intensity site also recorded an

increasing similarity with the reference site although the trend is rather fluctuating for biomass. During the entire period of the study, both high and low dredging intensity sites were significantly different from the reference sites.

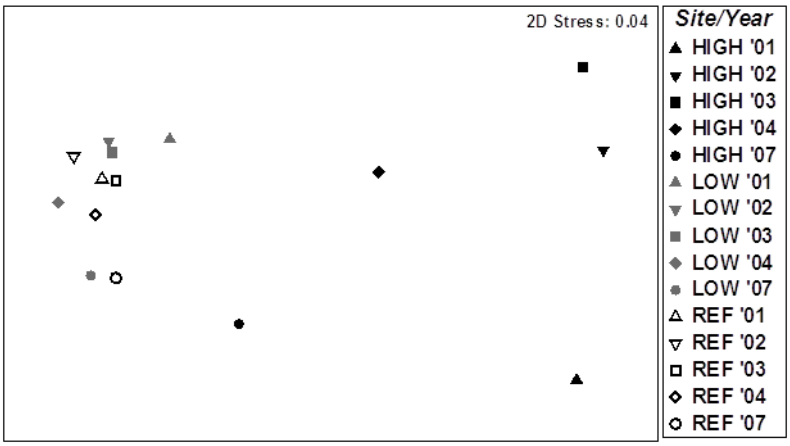

Figure 3.2. An MDS plot of Bray-Curtis similarity based on square root transformed data of abundance at sites of high and low dredging intensity and the reference sites.

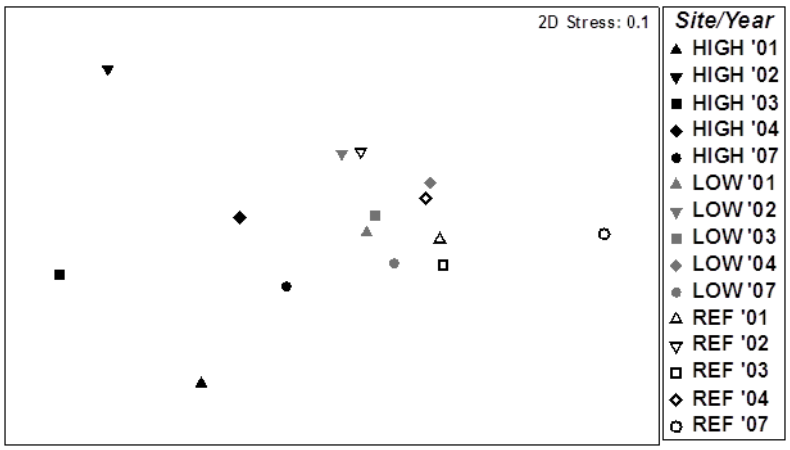

Figure 3.3. An MDS plot of Bray-Curtis similarity based on square root transformed data of biomass at sites of high and low dredging intensity and the reference sites.

Table 3.2: Summary of R-values derived from ANOSIM test based on values from abundance (N) and biomass (B).

Technique	High/Ref	Low/Ref
N		
2001	0.787*	0.486*
2002	0.890*	0.467*
2003	0.518*	0.394*
2004	0.500*	0.397*
2007	0.456*	0.290*
B		
2001	0.733*	0.264*
2002	0.669*	0.433*
2003	0.546*	0.312*
2004	0.420*	0.362*
2007	0.417*	0.357*

* Significant difference at $p < 0.01$.

3.3.2 Macrofaunal inventory and species diversity

Over half of the macrofaunal community in Area 222 was represented by Polychaetes, with 53% (14,741 ind.) of the total number of individuals. Crustaceans were second in the dominance order with 21% (5,715 ind.) of the total abundance, followed by Echinoderms and Molluscs, which, contributed to 9.4% (2,601 ind.) and 7.7% (2,148 ind.) of the total abundance respectively. The remainder of the total abundance was made up by the 'others' group including Cnidarians, Nemerteans, Nematodes and Tunicates. The order of the most abundant taxa by site recorded a fairly similar trend, with Polychaetes recorded as the most abundant followed by Crustaceans, Echinoderms and Molluscs (Figure 3.4). A slight difference was only recorded for the high intensity site where Molluscs were recorded as the second most dominant taxa.

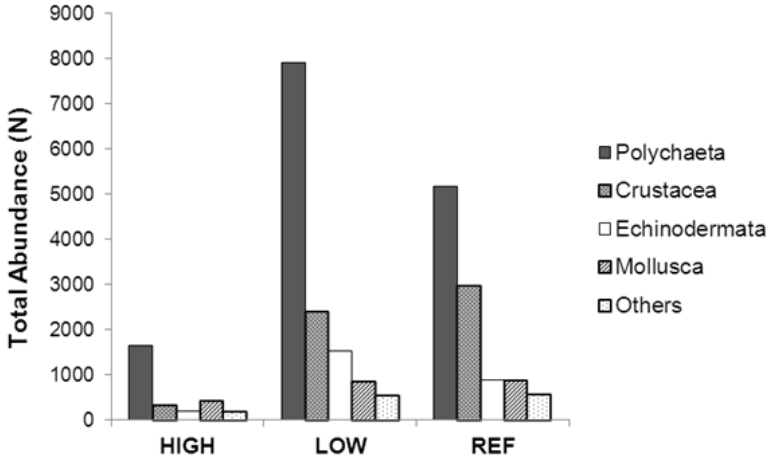

Figure 3.4. Total abundance of major taxa at sites of high and low dredging intensity and the reference sites over the study period.

Polychaetes also comprised of the highest number of species with 139 (32.3%) of the total of 430 species found during the course of the study. With 112 species (26%) of the total number of species, Crustaceans emerged as the second most diverse taxa. This was followed by Molluscs with 73 species (17%), Bryozoans (39 species – 9.1%), Echinoderms (19 species – 4.4%) and Cnidarians (18 species – 4.2%). The 'others' group of mainly Tunicates and some species from Nemerteans, and Nematodes complete the list.

Differences in the distribution of species richness were clearly shown at the high dredging intensity site compared to the low intensity and reference sites. Of the 430 species found during the study period, 258 species were recorded at high intensity site, while both the low intensity and reference sites were inhabited by 324 and 318 species respectively. The site with higher dredging intensity clearly recorded a lower number of species compared to the reference site, while the difference was less apparent for the low intensity site. The number of species also showed clear difference for both dredged sites. At the high intensity site, the number of species was fairly consistent from 2001 to 2003, followed by a marked increase of 63% in 2004. In contrast, the increase was less apparent at the low intensity site with the highest increase (from 2003 to 2004) only 29%.

Table 3.3. Total number of species (S) recorded at each sites during the study period.

	Site	2001	2002	2003	2004	2007	Total
No. of species	High	79	96	89	145	140	258
	Low	134	151	150	193	212	324
	Ref	162	190	153	198	185	318

No significant difference (one-way ANOVA: $p > 0.05$) was recorded for species richness over time at the reference site (Figure 3.5). In general, the high intensity site consistently recorded lower (significant at $p < 0.05$) mean values compared to the low intensity and reference sites. The number of species at the low intensity site shows no significant difference from the reference site. Mean values of species at the high intensity site showed a fairly constant increase from the start to the end of study with the exception of 2003 where the value was lower than in 2002. The mean values recorded at the low intensity and reference sites were more variable during the study period.

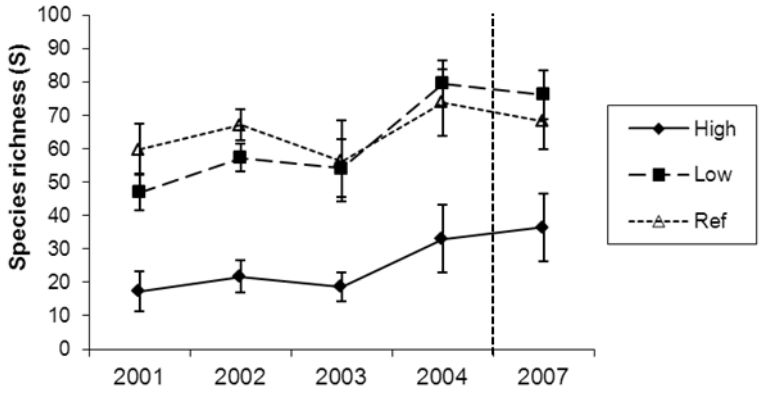

Figure 3.5. Summary of means and 95% confidence intervals for the number of species at sites of high and low dredging intensity and reference site. The dotted vertical line indicates the discrepancy in time intervals.

Overall, the polychaete *Pomatoceros lamarcki* was the most numerically important species at Area 222, dominating the taxa at both the high and low dredging intensity sites (Table 3.4). It was the second most dominant species recorded at the reference site. The composition of the 5 most dominant taxa at the high intensity site were very different to the reference site with only two similar dominant taxa (*P. lamarcki* and Serpulidae) recorded at both sites. In contrast, with four major taxa recorded at both sites, the resemblance between the low intensity and reference sites were more pronounced. *P. Lamarcki* was the species which contributed most to the differences

between the high intensity and reference sites, and the low intensity and reference sites. The second most influential species was *Pisidia longicornis*. Other species, for example, *Lanice conchilega, Lumbrineris gracilis* and *Scalibregma inflatum* were also influential in this respect (Table 3.5).

Table 3.4. List of the 5 most dominant taxa (based on total abundance) in Area 222.

HIGH	Taxa	2001	2002	2003	2004	2007
Pomatoceros lamarcki	Polychaeta	1	4	15	81	379
Spisula (juv.)	Mollusca	39	66	3	12	27
Spisula solida	Mollusca	41	66	3	12	2
Serpulidae	Polychaeta	-	3	5	35	73
NEMERTEA	Nemertea	11	28	15	25	23

LOW	Taxa	2001	2002	2003	2004	2007
Pomatoceros lamarcki	Polychaeta	43	349	803	1820	609
Pisidia longicornis	Crustacea	89	430	152	598	82
Serpulidae	Polychaeta	20	87	182	468	76
Ophiura (juv.)	Echinodermata	36	33	129	334	86
Lumbrineris gracilis	Polychaeta	36	75	105	168	89

REF	Taxa	2001	2002	2003	2004	2007
Pisidia longicornis	Crustacea	368	919	116	290	21
Pomatoceros lamarcki	Polychaeta	336	255	388	298	82
Lanice conchilega	Polychaeta	545	15	6	4	85
Serpulidae	Polychaeta	137	78	141	163	8
Lumbrineris gracilis	Polychaeta	93	126	109	113	85

Table 3.5. Average dissimilarity between two samples derived from SIMPER analysis.

	2001	2002	2003	2004	2007
HIGH vs REF					
Pomatoceros lamarcki	5.22	3.93	5.56	3.09	2.95
Pisidia longicornis	5.12	6.72	2.40	3.99	-
Lumbrineris gracilis	2.34	2.48	2.40	2.03	1.53
Serpulidae	-	2.21	3.41	2.38	1.44
Lanice conchilega	5.39	-	-	-	1.66
Amphipholis squamata	3.59	2.20	-	-	-
Scalibregma inflatum	-	-	3.07	-	-
Actiniaria	-	-	-	-	2.04
Ophiura sp.	-	-	-	1.78	-
LOW vs REF					
Pomatoceros lamarcki	2.44	1.04	2.03	2.16	2.82
Pisidia longicornis	2.02	2.33	1.57	1.45	0.93
Scalibregma inflatum	1.00	0.80	-	1.05	-
Serpulidae	1.74	-	0.96	1.57	1.14
Ophiura sp.	-	-	1.26	1.69	-
Lanice conchilega	1.91	-	-	-	-
Praxillella affinis	-	0.70	-	-	-
Actiniaria	-	-	-	-	1.28
Verucca stroemia	-	-	0.94	-	-
Notomastus sp.	-	0.92	-	-	-
Anthura gracilis	-	-	-	-	0.85

Two diversity indices used in this study recorded rather different values in quantifying the diversity of the macrofaunal communities at each site (Figure 3.6). Margalef index (Dm) showed that the high intensity site was significantly different from the reference site throughout the study period (one-way ANOVA: $p < 0.05$), while no significant difference was recorded at the low intensity site ($p > 0.05$). The values of Dm showed a fairly similar trend with the mean values of species richness. On the other hand, analysis using Simpson index (Ds) revealed that both the high intensity and reference sites were similar from 2001 to 2004, but appeared to be different in 2007. Meanwhile, the low intensity site was more varied where the values show a steep decline from 2002 to 2004, but then increased again in 2007. This trend might be due to the high abundance of *P. lamarcki*, particularly in 2004 that reduced the values of the index which is based on both number of species and abundance of each species.

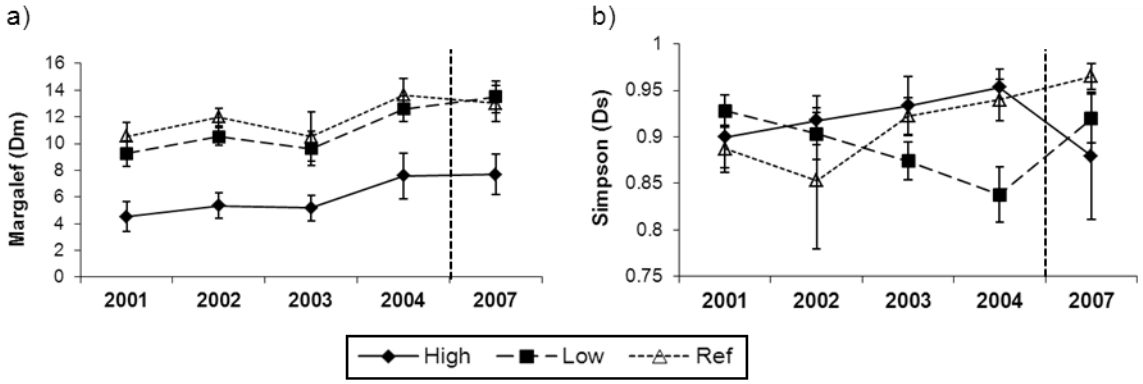

Figure 3.6. Mean values (±95% confidence intervals) of a) Margalef index and b) Simpson (complement) index at the high and low dredging intensity sites and reference site from 2001 to 2007. The dotted vertical line indicates the discrepancy in time intervals.

Rarefaction plots showed that the number of species at the high intensity site was not necessarily the lowest for all years (Figure 3.7). In 2001 and 2002, the highest species richness was recorded at the high intensity site. However, in the next two years the highest species richness was recorded at the reference site. The difference between sites was apparent in 2001 to 2004. However, in 2007, species richness showed a smaller difference between sites indicating that by this year, the number of species at the high and low intensity sites were progressing towards similarity with the reference sites.

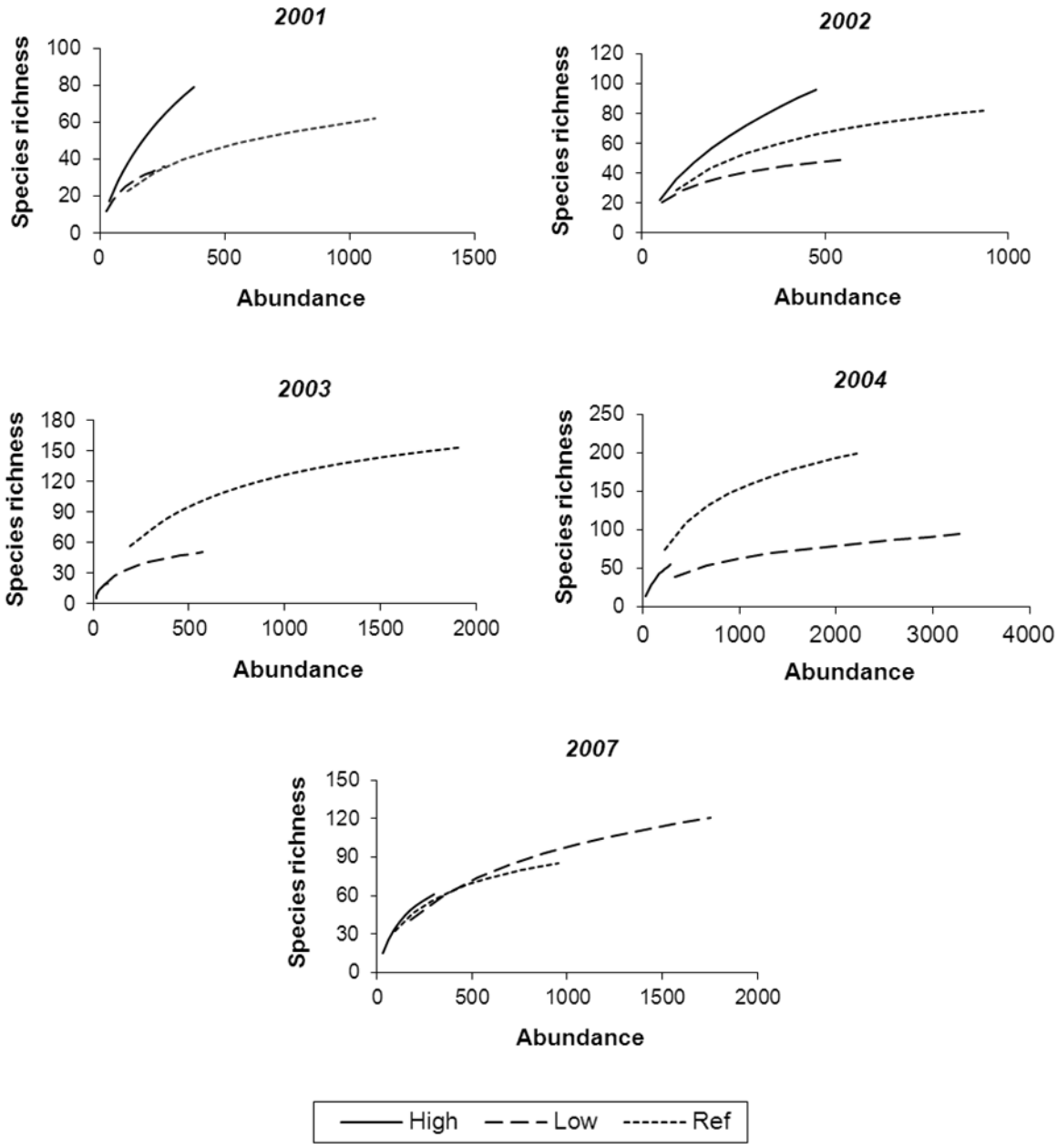

Figure 3.7. Rarefaction curves show the number of species at the high and low dredging intensity sites and the reference sites after been re-scaled based on the lowest abundance values.

3.3.3 Beta diversity

A time series comparison of beta diversity showed the high intensity site was generally higher between times than the other sites (Table 3.6) indicating that species composition at this site was in a state of flux. (i.e. different sets of species over the period of study). The highest species turnover was recorded between 2003 and 2007 (βw = 0.58) while samples between 2002 and 2003 recorded the lowest degree of

similarity with βw = 0.38. At the low intensity site, the pairing that involved year 2007 also recorded the highest value where the species turnover between 2002 and 2007 was βw = 0.43. A similar trend was recorded at the reference site where the highest turnover was recorded between 2001 and 2007, and 2002 and 2007 (βw = 0.35).

Beta diversity values between the high intensity and reference sites were generally higher than between the low intensity and reference sites (Table 3.7). The highest diversity between the high intensity and reference sites was recorded in 2001 (βw = 0.68) with the values decreasing over time to the lowest (βw = 0.48) in 2004 and 2007. A fairly similar trend was recorded at the low intensity site where the highest beta diversity was recorded at the start (βw = 0.60) while the lowest value (βw = 0.36) was at the end of the study. The only anomaly was between 2002 and 2003 when the value plummeted to βw = 0.44 and then increased in the following year at βw = 0.58.

Table 3.6. Whittaker's measure of diversity (βw) within sites over the period of study.

HIGH					
	2001	2002	2003	2004	2007
2001					
2002	0.53				
2003	0.52	0.38			
2004	0.53	0.48	0.45		
2007	0.53	0.55	0.58	0.44	

LOW					
	2001	2002	2003	2004	2007
2001					
2002	0.29				
2003	0.27	0.29			
2004	0.34	0.33	0.34		
2007	0.42	0.43	0.40	0.35	

REF					
	2001	2002	2003	2004	2007
2001					
2002	0.30				
2003	0.25	0.31			
2004	0.30	0.31	0.31		
2007	0.35	0.35	0.33	0.31	

Table 3.7. Comparison of Whittaker's measure of diversity (*βw*) between sites from 2001-2004 and 2007.

	High/Ref	Low/Ref
2001	0.68	0.60
2002	0.60	0.44
2003	0.60	0.58
2004	0.48	0.39
2007	0.48	0.36

Ordination by cluster analysis shows that the species turnover were different between sites (Figure 3.8). The higher value of beta diversity at the high intensity site is shown by the higher dissimilarity value (0.53) of the dendrogram. The low intensity site recorded a lower degree of variability over the period of the study than the high intensity site with dissimilarity value of 0.47, while the variability at the reference site was the lowest (dissimilarity = 0.31). The low intensity site showed a higher resemblance to the reference site with a dissimilarity value of 0.47, while the dissimilarity between the high intensity and reference sites was 0.60. The highest resemblance between dredged and undisturbed sites was recorded at the Low site in 2007 with 0.38 dissimilarity value.

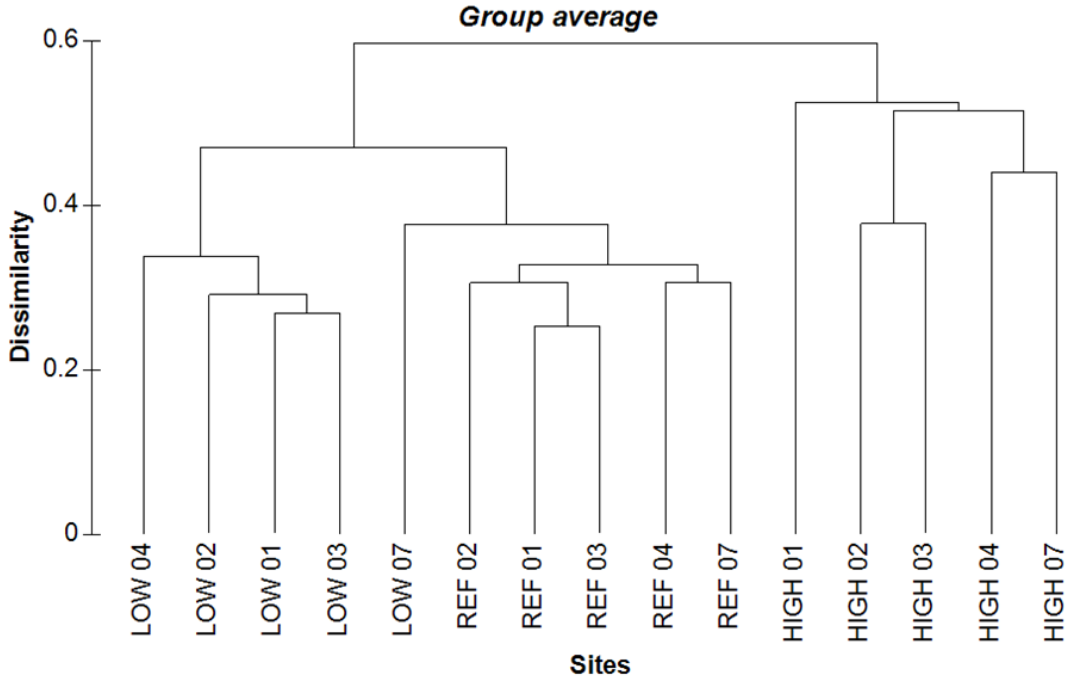

Figure 3.8. Ordination dendrogram of the dissimilarity of the sites over the study period based on the value of Whittaker's beta diversity.

3.3.4 Taxonomic distinctness

Taxonomic distinctness (TD) values at dredging sites were consistently lower than the reference sites throughout the study period, but were only significantly lower ($p < 0.05$) in the 2001 (high intensity site) and 2007 (low and high intensity sites) (Figure 3.9). The reference site had higher TD values in accordance to the higher number of species that this site accommodated. A relationship between species richness and TD was not always the case for both dredged sites as sometimes the high intensity site showed higher TD values although this site consistently had fewer species. The higher values at this site showed that it accommodated a more taxonomically diverse community than both the low intensity and reference sites. This trend was confirmed by the distribution of the samples in a funnel plot (Figure 3.10). Samples from the high intensity site are skewed toward the left hand side of the funnel plot indicating a low number of species at this site. Meanwhile a higher number of species at the low intensity and reference sites skewed the samples from both sites to the right hand side of the plot. Although there are several samples grouped outside the funnel lines, the grouping of most of the samples (including the high intensity site) inside the lines suggests that there was no significant change of the taxonomic distinctness.

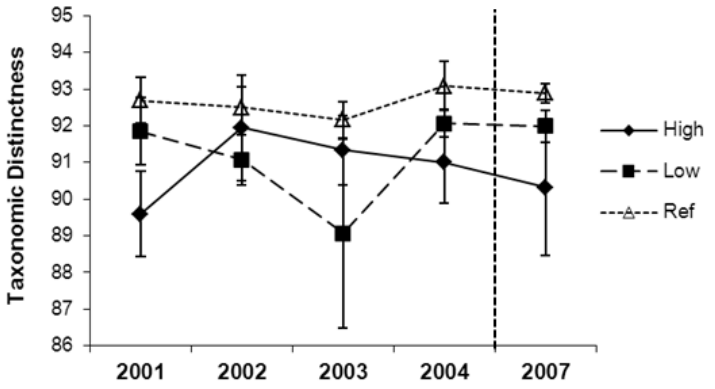

Figure 3.9. Annual mean values (±95% confidence intervals) Taxonomic High and Low intensity dredging sites and Reference site. The dotted vertical line indicates the discrepancy in time intervals.

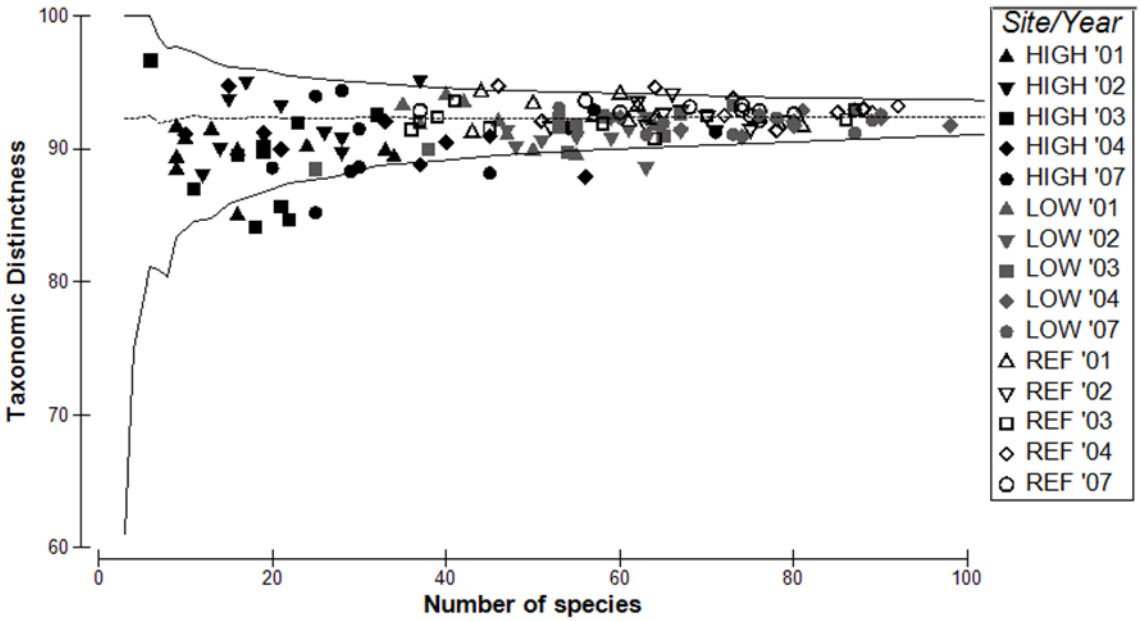

Figure 3.10. Funnel plot for Taxonomic Distinctness (TD) of high and low dredging intensity sites and reference site. The funnel plot graphs the distribution of assemblages based on the number of species in every station. The mean TD of the whole assemblage is represented by the dotted horizontal line, while the funnel lines indicate the 95% confidence limits.

3.3.5 Predictive time of recovery at the high dredging intensity site

The time taken for the community at the high intensity site to fully recover was predicted based on abundance, biomass, species richness and Margalef index. Most of the indices suggested the full recovery to occur from 13 – 15 years (exponential fitting line) and 18 – 19 years (linear fitting line) after dredging (Figure 3.11). In contrast, the recovery based on biomass index was predicted to occur in the following ~10 (exponential) and ~30 years (linear).

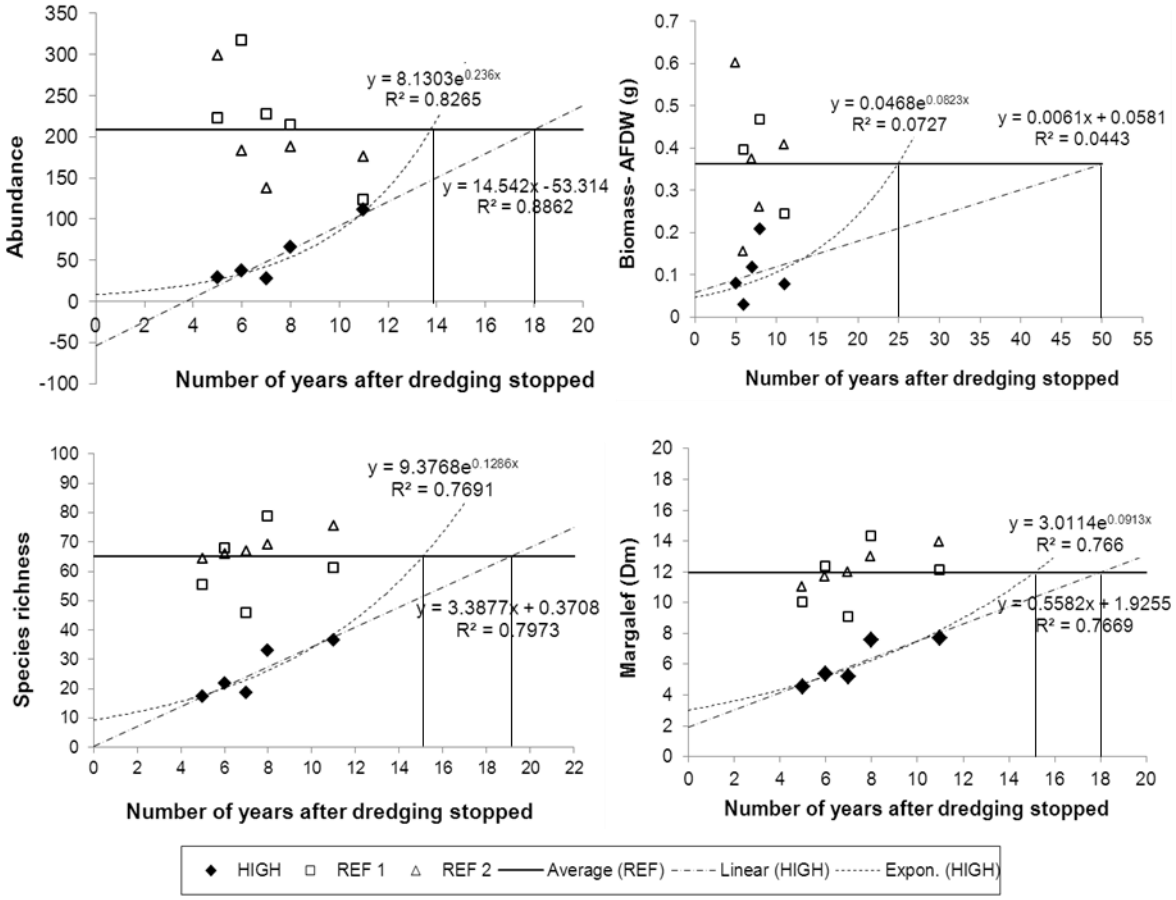

Figure 3.11. Trajectory of predictive time of macrofaunal recovery at the high dredging intensity site based on different traditional statistical measurements.

3.4 Discussion

3.4.1 Abundance and biomass

Naturally, benthic community structure in Area 222 was fairly comparable (in terms of abundance and biomass) to the other dredging sites in the UK and nearby areas such as in the East Coast of the UK (Barrio Froján et al., 2008), Dieppe, English Channel (Desprez, 2000) and Ravenna, Northern Adriatic (Simonini et al., 2007). As in those areas, the undisturbed site in Area 222 was dominated by *r*-selected species (e.g. *Pomatoceros lamarcki*, *Pisidia longicornis* and *Lanice conchilega* (Barrio Froján et al., 2008; Claveleau and Desprez, 2009)) which are characterised by showing rapid recolonisation (Kenny and Rees, 1996) and high dispersal potential (Barrio Froján et al., 2008). The dominance of *r*-selected species was also reported in other studies in dredging areas (e.g. Desprez 2000; van Dalfsen and Essink, 2001; Cooper et al., 2007; Moulaert and Hostens, 2007; Barrio Froján et al., 2008).

As expected, the abundance of macrofauna at dredged sites (particularly at the high dredging intensity site) in the present study showed a significantly lower value than at the undisturbed site over the study period. This shows that due to their low mobility (as opposed to other fauna such as fish and marine mammals), the benthos is easily removed during the dredging process (Newell et al., 1998) and their response is, to a degree, predictable. In addition to faunal removal through dredging, the low abundance of macrofauna at the high intensity site also suggested that remaining benthic fauna is susceptible to various stresses (Pearson and Rosenberg, 1978; Dauer, 1993) that cause injury or death to the fauna (Hall, 1994). While the negative impact of dredging was evident at the high intensity site, the site with lower dredging intensity was less affected; yet interestingly also recorded an increase in species abundance, particularly in 2004. As there was no significant variation (one-way ANOVA: $p > 0.05$) at the reference site over the course of study, it is assumed that natural variability was not the causative factor responsible for the higher abundance of macrofauna at the low intensity site. The trend was however more likely due to the successional changes that were going on at this site (Boyd et al., 2004). This is true when considering that the abundance was substantially increased from 2003 to 2004, but again, reduced in 2007.

Due to the fact that benthic macrofauna have a wide range of different body sizes, the use of abundance alone is not sufficient in describing the changes of macrofaunal structure and related function (see Chapter 7). Therefore, in this sense, biomass is important as a complimentary measure to abundance. In the present study, the macrofaunal community at the high intensity site also appeared to be impacted by dredging in term of biomass, judging from biomass being consistently lower than the reference sites. In contrast, dredging activity did not affect the biomass at the low intensity site. Nonetheless, this trend still showed an interesting point to relate the abundance and biomass with the successional changes at the low intensity site. According to Dauer (1993) and Ritter (1999), lower biomass and dominance of characteristic species can be regarded as the main features of early successional communities. Clearly data from the present study support this finding. The significantly high abundance of macrofauna at the low intensity site in 2004 was disproportionate to the biomass value. It is assumed that this trend could be due to the dominance of *Pomatoceros lamarcki,* which, as characterised by small-bodied *r*-selected species (Claveleau and Desprez, 2009; but see Gray and Elliott, 2009) had

substantially increased total abundance, but at the same time the biomass was not proportionately increased. While it was still significantly higher than the reference site, the reduction of abundance in 2007 may suggest that the macrofaunal community was progressing towards the late succession stage where the community should be comprised of larger and slow growing species.

Multivariate analyses revealed that the high dredging intensity had caused greater changes for both abundance and biomass as compared to the changes imposed by a lower dredging intensity. In addition, the analyses also show that samples at the high intensity site recorded the highest variability within the site. This was in contrast to the samples at the low intensity and reference sites which both had higher levels of within-site similarity. This pattern could provide the insight that the higher level of dredging intensity had caused high density of dredge trails and consequently the macrofauna became unevenly distributed with patches of high and low biodiversity. The pattern at the high intensity site was at least in accordance to the study by Connell (1978) who suggested that the distribution of disturbance effects are patchy in space and time, and the patches developed through different stages of the successional process. As far as the distribution pattern of the samples is concerned, the high intensity site is perceived as impacted and could still be at a very early stage of succession. However, for a more optimistic view, there may be progress towards recovery that was underway starting from 2004, judging from the close distance of the samples from this site with the samples from the reference site. In contrast, the ordination pattern of samples from the low intensity site suggests that the assemblage at this site was more evenly distributed and may have recovered by the time the sampling took place. It is true that the R value of ANOSIM still described the site as dissimilar to the reference site, but to suggest this site has not recovered could be misleading as the dissimilarity was due to a significantly higher number of individuals at the low intensity site (refer to the mean Abundance value). The identical pattern of samples distribution is shown for biomass, and this leads to a similar conclusion in terms of successional process and the recovery of the community at both sites. Again, the bizarrely high abundance at the low intensity site might also have caused the dissimilarity (ANOSIM R-value) of the biomass with the reference site.

3.4.2 Species richness and diversity

The composition of macrofauna in Area 222 conforms to the other studies in areas subjected to dredging (e.g. Boyd et al., 2003; Cooper et al., 2007; Moulaert and Hostens, 2007; Barrio Froján et al., 2008). Polychaetes remain as the most dominant group even after a high intensity of disturbance. The reason might be due to the fact that Polychaetes are comprised of mainly *r*-selected species that have a rapid recolonisation rate, thus helping them to return rapidly as the most dominant group. On the other hand, Echinodermata, which comprises mainly larger-sized fauna, seemed to be affected by the dredging to the point that their dominance was reduced disproportionately compared to Crustacea and Mollusca (which have a smaller body size). The other reason that Polychaetes may be less susceptible to physical disturbance could be due to their higher diversity which helps them to be more tolerant to different types and levels of pressure (Dauer, 1993). Subsequently, this might increase the likelihood of this group survivingin a damaged habitat.

Dredging intensity changed the species richness in the present study where it was significantly lower at the site with higher dredging intensity. This trend was also apparent in terms of abundance and biomass, at least for the high intensity site. In contrast, low dredging intensity did not change the number of species in this study. Although widely used in various areas of study, species richness may have a disadvantage due to its dependence on sampling effort (Magurran, 2004). One way to compensate the influence of sampling effort is by dividing R with the number of individuals, for example the Margalef index (Magurran, 2004). However, there was no clear difference between the value of this index and species richness at all sites over the study period. The only small difference was recorded at the low intensity site in 2004. The species richness at this site was higher than at the reference site (this is obviously expected as the abundance at the low intensity site was significantly higher than at the reference site). However, by compensating for sampling effect, Margalef index produced a contrasting result in that particular year. The effect of sampling could also be seen when the macrofaunal assemblage data was subjected to rarefaction. Like the Margalef index, this method diminishes the effect of sampling in order to determine species richness (Magurran, 2004). It is based on the principle that, if a sample is collected from an area with a high number of individuals, the number of species is more likely to be high. Likewise, the opposite possibility is true if a sample is collected from an area with lower abundance, because the rare species

are less likely to be recorded (Gotelli and Colwell, 2001). Clearly there was an effect of sampling in this study as the rarefied number of species at the most impacted area (i.e. the high intensity site), did not always show the lowest number of species. In fact, the highest number of species in the early years of study (i.e. 2001 and 2002) was recorded at this site. The high value at this site should probably not be regarded as recovery since the following years the value dropped again. However, judging from more stable plots in 2007, or in other words, the number of species drawn from the same number of individuals were fairly similar at all sites, it can be assumed that the recovery in term of species richness had taken place at both dredged sites. Although rarefaction is a good technique for measuring the number of species that is corrected for sampling effect, the limitation of this technique needs to be considered. Rarefaction could be biased if applied to data which comprise samples with significantly different species abundance distributions (Magurran, 2004); which is the case in the present study where the number of individuals of dominant species *Pomatoceros lamarcki* was over 1000 while many other species were only encountered once in the whole sample.

Simpson index incorporates both number of species and distribution of individuals for every species. Rather than provide the true diversity of a sample, Simpson index is regarded as an evenness measure. The advantage of this index is its robustness and lack of sensitivity to sampling effect (Magurran, 2004). Although there was a clear difference of species richness between the high and low intensity sites, the difference was less apparent based on Simpson index. At the start of the sampling in 2001, all sites recoded a similar diversity value regardless the degree of disturbance but began to vary from 2002. There is one possible explanation that can be offered with regard to this. The effect of dredging had proportionately reduced both number of individuals and species at both dredged sites. Therefore the community remained proportionally even in terms of the proportion of the number of species and the number of individuals. This might explain why the values at these sites in 2001 were still the same as the reference site. For the low intensity site, the value started to show a decrease trend in 2002, and it became obvious in 2003 and 2004 before increasing again in 2007. This trend might reflect the succession at this site in 2003 and 2004. This site was dominated by several species (opportunistic or *r*-selected species) that as a whole had reduced the evenness of the community. The increase of index value in 2007 therefore might suggest the final stage of succession where the other species

have returned to reduce the influence of opportunistic species and thus the community became more even. In contrast, a sudden decline of the index value at the high intensity site might suggest this site was about to undergo a successional process in 2007.

3.4.3 Diversity over space and time

The pattern of species distribution in the present study was also impacted by dredging activity. While alpha diversity only relates to the number of species without the information of the species identity, beta diversity gives further information with regard to how similar the set of species are between sites or over time. High dredging intensity was associated with a high degree of dissimilarity between samples. As recorded at the high intensity site, the variability in species composition over time was higher compared to such variability at the low intensity and reference sites. The Whittaker index values show that after a series of disturbances, the high intensity site was inhabited by a different (in the sense that it was more different than other sites) group of species every year. The reason for this might be due to instability of the environment at this site that stopped many mobile species from establishing, which instead moved out to the more stable nearby areas. In contrast, a more stable low intensity site (due to less damage imposed by low dredging intensity) was able to accommodate more species, hence support a more similar group of species. Dredging not only created a high variability of groups of species over time, but it also created a less similar group of species in comparison with the pre-dredged state. In this case, once again, the impact of dredging intensity was obvious where the dissimilarity between high intensity and reference sites was higher than between the low intensity and reference sites. However, the decrease value of this index might give an insight to the progress towards recovery at both sites although the progress at the site of low dredging intensity was at a faster rate. This is supported by the dendrogram (Figure 3.8) that shows the community at the low intensity site in 2007 became more similar to the community at the reference site.

3.4.4 Taxonomic distinctness

As discussed above, one major problem of incorporating the abundance data in determining species diversity is the likelihood that a higher number of species will be encountered at an abundance-rich area. Therefore, to eradicate this problem, Taxonomic Distinctness (TD) index can be a good solution. The result seems to

accord with the other diversity indices recorded for the low intensity site, where this site still accommodates a high number of species even after disturbance. In contrast, the TD value also revealed that the high intensity site was similar to the reference site although this site was inhabited by a lower number of species than the other two sites. This strange TD property at the high intensity site might be explained by the competition between species within similar higher taxonomic groups. For instance, a limited amount of food as a consequence of disturbance might force the species to be more aggressive to survive in the area. This creates a more intense competition that leads some species with similar characteristics, especially feeding mechanism, to move to other less competitive areas. This could theoretically generate the removal of species that share traits and might be expressed evenly across taxa. The strong competition might favour the addition of other species with no similar characteristic. Thus, maintaining this site's taxonomic diversity as it was before dredging took place.

3.4.5 Comparison of different techniques

It is fairly understandable that different techniques produced different recovery times for the dredging sites. However, these techniques appeared to suggest that a faster recovery was underway or has already taken place at the site with a lower dredging intensity. In addition, all techniques used were also able to discriminate the high intensity site from the other two sites, where the suggested recovery occurred later or in some cases had yet to happen. Simpson index was the only technique that was not able to highlight the fact that high dredging intensity led to a more severe impact to the site, so much so that this index also indicated that the recovery at this site was first to occur (5 years after dredging ceased) compared to the other indices.

Clearly, the results suggest that in order to get a better understanding of dredging impact on the benthic community, different techniques which are based on different foundations should be used concurrently to complement each other. The use of abundance may be less meaningful on its own without additional information about biomass. Together with abundance, biomass data is useful to clarify whether a community has truly recovered when both indices recorded a comparable increase. In cases where an increase in abundance is not proportionate with a similar increase in biomass, the community might be classified as in successional stage (i.e. comprises of high number of small-bodied fauna). Another useful measure to assess the community is diversity and maintenance of diversity is important as different

species contribute different roles to the system. The simplest measure of diversity (species richness) was the actual number of species at each site. Understandably, this index suggested that the high intensity site was still far from reaching the recovery state. However, this could be due to sampling effect (i.e more species recorded due to higher abundance) as the rarefied data the community at this site in 2007 was as diverse as the community present within the reference site if the data were corrected for sample size. The finding from rarefaction was supported by the Simpson diversity index which also suggested that the recovery of community at the high intensity site had already taken place. Meanwhile, β-diversity (Whittaker index) provides an interesting insight into comparative diversity as this index distinguishes the commonness in species identity between samples. Using this measure, assemblages with no shared species are considered more different than assemblages with many species in common. To put this into perspective for the present study, the high intensity site appeared to have more different sets of species (biodiversity stock) over the years, and this site also shared a low number of species in common with the reference site. One could argue that after a series of disturbance, the community composition at the high intensity site had changed to be different from the reference site, and this could lead to a conclusion that this site was much more impacted than the low intensity site which appeared to have more species in common with the reference site. However, the necessity for a disturbed site to have a similar community composition to that of a reference site, in order for it to be considered as having recovered remains an open question (will be discussed later in Chapter 4). Obviously, an advantage of β-diversity is its independence from sampling effect, and this criterion is also a strong point in favour of Taxonomic Distinctness (TD). This index is more sophisticated as it takes into account the whole level of phylogeny or taxonomic classification. Therefore it manifests a more defined form of diversity since, for example, if two assemblages have the same number of species, the assemblage which contains species from different taxa (of higher taxonomic group, e.g. Family) will be more diverse than the assemblage which contains species from a single taxon. TD provides collective information of how a community is affected by disturbance, for instance through the taxa's response to stressors (Bremner et al., 2003). Another advantage of this index is it produces funnel plot with 95% confidence intervals to facilitate the interpretation of diversity, i.e. samples within the funnel lines are considered to be equally diverse regardless of the number of species recorded. However, this kind of index, which is not associated with abundance data, might be

regarded as less sensitive. As shown in the present study, the abundance at the high intensity site was consistently lower than the other sites from 2004-2007, but yet the TD value did not show the same trend.

The prediction of fully recovery at the high intensity site was consistent based on most of the traditional indices, with the exception of biomass which predicted a significantly longer time to recovery than the other indices. The abundance, species richness and Margalef index provided comparable predictive times and with a fairly high value of confidence (i.e. high R^2 value). This indicates that the prediction of recovery can be based on these indices. In contrast, the prediction of recovery in terms of biomass should be treated with care (very low R^2 value). This extremely long predicted recovery period may be the result of the high variability of the samples within the reference site which subsequently produced a high average value of biomass. At the same time, this trend may also have been exacerbated by the variability of the samples within the high intensity site. The consequent result was that the best fit lines were weighted towards the substantial decrease of biomass at the high intensity site. In addition, the prediction based on biomass may be misleading if the successional phase of the community is taken into account.

3.5 Conclusion

Benthic communities in Area 222 were within the range of community structure observed in other nearby areas. However, after disturbance Area 222 was different to those areas. This is due to the difference in dredging frequency that every area had experienced. Similarly, the sites within Area 222, which were subjected to different dredging intensity, also developed a different community structure. In the present study, all three common traditional measures, namely abundance, biomass and species richness appeared to show that high dredging intensity caused more damage to the environment than the lower intensity did. However, more current and advanced techniques such as rarefaction, diversity indices and Taxonomic Distinctness suggested that the impact caused by both dredging intensities was fairly similar. However, the immediate impact after the dredging ceased might be different.

The present study also showed how different intensities of dredging can lead to different times for the community to recover once the stress is removed. More importantly, the interpretation of recovery periods was related to different biological

measurements. However, in general, low dredging intensity did not appear to impose great impacts on benthic community (in certain cases it may have favoured the community), while high dredging intensity showed lasting damage. Different findings from various techniques showed how important it is that many biological aspects should be considered in order to assess macrofaunal community structure. However, it is not feasible to always apply multiple measures in every study. Therefore, for the purpose of ecosystem management, the definition of recovery has to be made based on expert opinion on the question of what kind of recovery is required, whether the quantity, biomass or diversity; or all of these criteria and this has to take into account other potential modes of exploitation of the systems (e.g. fisheries, leisure and aquaculture).

Declaration

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Chapter 4: Assessment of ecosystem function using functional traits analysis

4.1 Introduction

For many years, the effect of disturbance has been assessed using traditional metrics such as abundance, number of species and biomass (Johnson and Frid 1995; Newell et al., 1998; Boyd et al., 2004; Cooper et al., 2005; Bolam et al., 2006). These assessments were carried out to determine the recovery of the ecosystem, which is defined as having taken place when secondary succession returns the ecosystem to the pre-existing state (Borja et al., 2010). However, since the dynamic nature of the seabed and physical disturbance alter the physical characteristics of the sediment, the original or pre-existing assemblage may no longer be able to be accommodated (Mathews et al., 1996; Desprez, 2000). Therefore, the use of traditional metrics should be treated with care when dealing with biological recovery as the assessment only incorporates the range and proportion of species present without taking into account the ecological and biological characteristics of the community. Mouillot et al. (2007) suggested that the extent to which species loss can alter basic ecosystem processes depends on the functional richness (i.e. the number of functional groups) in an ecosystem. In terms of dredging impact on functional diversity, communities of organisms inhabiting an area of dredged seabed possibly differ in composition or diversity from the pre-dredged state, but may develop similar functional capacity through the recovery process. Therefore, system recovery may not require similar biomass, biodiversity or community composition. This is due to possible functional redundancy, whereby the loss of a particular species doesn't affect ecosystem function since the function performed by that species is taken up by another species from the same functional group (Walker, 1992; Lévêque and Mounolou, 2003). To address this issue, many studies have recently focussed on functional diversity to assess faunal recovery following anthropogenic perturbations by incorporating biological differences among species (e.g. Maurer et al., 1999; Borja et al., 2000; Botta-Dukat, 2005; Bremner et al., 2006a, 2006b; Cooper et al., 2008; Josefson et al., 2009; Barrio Froján et al. 2011). Biological difference, which can be drawn from functional traits, is proved to respond significantly to human disturbance. Function- or trait-based diversity metrics may thus represent appropriate additional methods for assessing changes in ecosystem function (Péru and Dolédec, 2010).

Only recently the functional traits metrics were used in assessing the status of benthic community in the UK waters. Cooper et al. (2008) and Barrio Froján et al. (2011) have applied a number of these metrics (together with traditional metrics) for the assessment in Hastings Shingle Bank (English Channel) and Area 408 (off the Humber estuary) respectively. In Hastings Shingle Bank, where sediment composition between dredged and reference sites were comparable, the biological recovery based on functional diversity occured at a faster rate than when measured by traditional metrics. In contrast, Area 408 (sediment composition between dredged and reference sites was high) recorded no difference in terms of recovery rates between functional and traditional metrics (Cooper et al., 2088; Barrio Froján et al., 2011). Considering the fact that Area 222 is in the middle of the spectrum between Hastings Shingle Bank and Area 408 in terms of sediment composition, the present study was carried out to assess the recovery of the benthic community in the area where the sediment composition was moderately changed by the effect of dredging. In this chapter, the recovery of dredged sites in Area 222 was assessed using five functional indices. These indices were Somatic Production, Infaunal Trophic Index, Biological Traits Analysis, Rao's Quadratic Entropy and Functional Diversity. The principle method of assessment is similar to that presented in the previous chapter, where the community at both dredging sites were compared to the undisturbed sites over time. This chapter provides a comprehensive comparison of the characteristics and performances of different functional indices applied to the dredging data. In addition, the use of functional indices offers a different perspective on recovery. This is particularly useful when physical changes resulting from dredging mean that the original assemblage may no longer be able to be accommodated.

4.2 Methods

4.2.1 Functional traits analyses

From a review of 12 functional analyses to quantify functional diversity that Cooper et al. (2008) examined, they recommended 4 techniques as suitable for use with a macrofaunal dataset acquired from an aggregate extraction site. Given the similar nature of the present study, the same techniques were applied. The techniques were Somatic Production, Infaunal Trophic Index, Biological Traits Analysis and Rao's Quadratic Entropy. In addition, another recent technique, Functional Diversity was also used in this study following its suitability to be applied on the datasets.

4.2.1.1 Somatic Production

In terms of energy flow, Brey (2001) defined Somatic Production (Ps) as the part of the food consumption processes that change the biomass (B) of an organism with time, and subsequently would potentially be available as food for other organisms in the next trophic level. Production to biomass ratio (P/B) is generally used to describe the turnover of a population. This ratio is mainly affected by life history characteristics such as density, recruitment, age, life span (Cusson, 2005), and abiotic factors such as temperature and depth (Brey and Clarke, 1993).

Calculations of production were made based on abundance and biomass data per unit area. Using published conversion factors, biomass records for each taxonomic family were converted to energy values. The calculation continued with combining abundance and energy values prior to converting to production values using Brey's Multi-Parameter P/B-Model: Annual somatic production-to-biomass ratio of benthic invertebrate populations. The production value for each taxon was then combined to provide a production value for each sample (Brey 2001). The conversion factor databank and Multi-Parameter P/B-Model were downloaded from the Internet (http://www.thomas-brey.de/science/virtualhandbook).

4.2.1.2 Infaunal Trophic Index

The Infaunal Trophic Index (ITI) is a more targeted approach used to monitor the response of a marine environment to organic enrichment or flux based on the dominant feeding mechanisms (Maurer et al., 1999). ITI exclusively focuses on organisms' feeding type as it is considered to be one of the central processes where ecosystem function is expressed (Pearson and Rosenberg, 1987). It is acknowledged that there is another index, namely AZTI Marine Biotic Index (AMBI) (Borja et al., 2000), which also uses the principle based on the Pearson and Rosenberg model (Gray and Elliott, 2009). However, the first rule in AMBI is that it is not suitable to be applied on hard substrata. No such rule is observed for the ITI. However, while ITI is suitable for soft bottom community, there is no warranty of its suitability for dredging data (Warwick, 1993; Elliott, 1994; Maurer et al., 1999). As the present study is a continuation of work testing several indices for dredging data, ITI was selected. Determination of ecosystem status using this index is by assigning every species into one of four feeding mechanisms before the total number of individuals for each species is entered into a formula to generate an index representing the trophic

composition of the community. The four established feeding groups were: 1) suspension feeders, 2) suspension and surface detritus feeders, 3) surface deposit feeders, and 4) subsurface deposit feeders (Maurer et al. 1999). As its focus on organic enrichment, the suitability of this index for dredging data is not warranted (e.g. Warwick, 1993; Elliott, 1994; Maurer et al., 1999).

ITI values in the present study were calculated using a purpose-designed Excel programme. A species abundance-by-sample matrix was applied in this workbook and every species was assigned to different trophic groups (Word, 1979). Where the information for an individual taxon was absent, the trophic group was assigned based on a higher taxonomic level. Meanwhile, expert judgement was used to assign taxa with more than one feeding group. In this case, each taxon was assigned to only one group according to which was the most relevant to that taxon. The total number of individuals in each group was used to calculate this index using the formula:

$$ITI = 100 - \left[33 - 1/3\left(\frac{0n_1 + 1n_2 + 2n_3 + 3n_4}{n_1 + n_2 + n_3 + n_4} \right) \right]$$

where n_i is the total number of individuals in group i. ITI values ranging from 80 to 100 indicate a reference condition. Values from 60 to 80 indicate normal/unaffected condition, values from 30 to 60 represent a modified condition and values from 0 to 30 indicate a degraded or polluted condition (Maurer et al., 1999; Word 1979).

4.2.1.3 Biological Traits Analysis

Biological Traits Analysis (BTA) uses specific species traits and variation in the pattern of traits to assess the functioning of an ecosystem (Bremner et al., 2006b, Bremner, 2008, Marchini et al., 2008). This technique is based on habitat templet theory (Southwood, 1977) which suggests that habitats play an important role in evolving species' characteristics. As habitat variability controls the community structure, knowing the community's biological characteristics provides information on how the organisms respond to stress, and therefore the functional diversity status can be identified (Bremner et al., 2003). Biological traits, which are directly related to ecosystem structuring mechanisms, are able to directly illustrate the factors that drive the change in communities.

For the present investigation, a species-by-traits matrix was produced based on eight categories namely: Size, Larval type, Relative adult mobility, Body form, Degree of attachment, Adult life habit, Feeding habit and Habitat. Each of these categories contained several different traits. For example, the category of Adult life habit contained traits of 'sessile attachment', 'tube attachment', 'burrower' and 'crawler'. Species were assigned to each category using a 'fuzzy coding' procedure in the range from 0 to 3; with 0 being no affinity and 3 being high affinity (Chevenet et al., 1994). A scaling up was undertaken in order to obtain standardised scores where the sum of the value in the categories equalled one. This matrix was multiplied by species abundance-by-sample matrix to obtain a species trait-by-sample matrix (see Charvet et al., (2000)). This newly obtained trait matrix was then analysed using multivariate analysis.

4.2.1.4 Functional Diversity

Like BTA, Functional Diversity (FD) also uses various traits in the index calculation. FD measures the total branch length of a dendrogram, constructed from species trait classifications (Petchey and Gaston, 2007). In the same way, FD measures the extent of the differences of some traits in one species to the traits in other species (i.e. complementarity between species). Complementarity exists when there are differences between two or more objects (species). As the differences between species traits values increases, the complementarity between species also increases, hence resulting in higher FD (Petchey and Gaston, 2002). Number of species, number of functional traits, community composition and species identity are all contributing factors that collectively determine the FD. Measurement of the branch length is done at all hierarchical scales simultaneously, where species are classified to different traits individually without assigning the species to specific functional groups. This makes FD a continuous measure where the pair-wise distances can vary in continuum as new species are added to the system (Petchy & Gaston, 2002; 2006).

A similar traits matrix used for calculation of BTA was applied for FD calculation. Using the standardised traits matrix, there were three steps in calculating FD: 1) calculation of distance matrix based on Euclidean distance (this matrix contained the pair-wise distances between species in traits dimensions); 2) clustering the distance matrix then using the Unweighted Pair Group Method with Arithmethic Mean

(UPGMA) method to produce a functional dendrogram; 3) calculating the total branch length of the functional dendrogram. The calculations of all three steps above were done by referring to the code freely available from http://owenpetchey.staff.shef.ac.uk/Code/code.html (Petchey and Gaston, 2002; 2006). These calculations were carried out using the software R (R Development Core Team, 2008).

4.2.1.5 Rao's Quadratic Entropy

Botta-Dukat (2005) proposed a functional diversity index based on quadratic entropy (Rao, 1982) which measures the pair-wise distance of functional differences between species. This index, Rao's Q also incorporates the number of individuals present in the community. Rao's Q is a generalised form of Simpson diversity index and in its calculation, both diversity and dissimilarity elements are addressed (Petchey and Gaston 2002, Mason et al. 2003). Rao's Quadratic Entropy satisfies *a priori* criteria to be a suitable functional diversity index as it 1) utilises more than one trait, and 2) incorporates species abundance; making it able to treat functional types differently based on the abundance value (Botta-Dukat, 2005).

The calculation of Rao's Q used the similar traits matrix as in BTA. Once the traits matrix had been established, the first step was to measure the dissimilarity between species, which was based on the trait overlap between different species (Leps et al., 2006). Then, the measured dissimilarity was combined with the relative contribution of each species to the assemblage (based on the abundance) to produce the Rao's Q value. An Excel macro purposely designed by Leps et al. (2006) was used to perform all calculations.

4.2.2 Univariate and multivariate statistics

One-way Analysis of variance (One-way ANOVA) was used to test the significant difference between the mean values of all functional analyses (except the BTA) at all sites in each year. Functional similarity between sites was graphically presented on non-metric multidimensional scaling (MDS). This ordination was further tested using analysis of similarity (ANOSIM) to test the significant difference between the samples. Occasionally, analysis of similarity percentage (SIMPER) was used to determine the contribution of different functional traits or species to the dissimilarity between samples. As in Chapter 3, the recovery of macrofaunal community was also predicted

by fitting the best fit line (linear and exponential) on the samples (functional indices values) at the high dredging intensity site. These lines were compared to the linear line of the average value at the reference sites to determine the number of years needed by macrofaunal community to functionally recover (i.e. achieve the value similar to the reference sites). This prediction was made based on Ps, ITI, Rao's Q and FD.

4.3 Results

4.3.1 Somatic Production

Annelids (mostly polychaetes) were the taxon which comprised the highest proportion of the total annual production (Figure 4.1). This was followed by crustaceans, in particular the 'higher' crustaceans such as Amphipods and Isopods. The impact of dredging seemed to evenly affect the major group as Annelida remained as the highest contributor at both dredged sites with the only exception in 2002 (the low intensity site). On the other hand, crustaceans appeared to be more affected by higher dredging intensity where this taxon (which had the second highest production value) recorded much less production value compared to molluscs and 'others' groups. Mean total annual production at the high dredging intensity site was significantly lower than the value at the reference sites (one-way ANOVA: $p < 0.05$) (Figure 4.2). In contrast, the mean value at the low intensity site recorded a more comparable total annual production with the reference sites. The value was significantly lower ($p < 0.05$) in 2001, but then became similar in the following years. The only strange property recorded in 2004 when the mean value at the low intensity site increased substantially to be higher than the value at the reference site. In general, the mean value at all three sites became more similar by the end of the study period although the value at the high intensity site remained lower than at the other sites ($p < 0.05$).

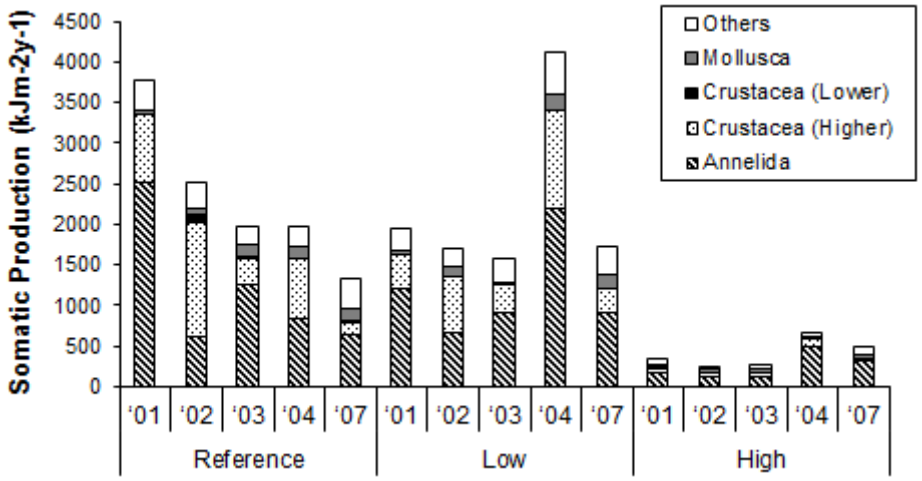

Figure 4.1. The proportion of total Somatic Production by major group at the high and low dredging intensity sites and reference sites from 2001 to 2004, and in 2007.

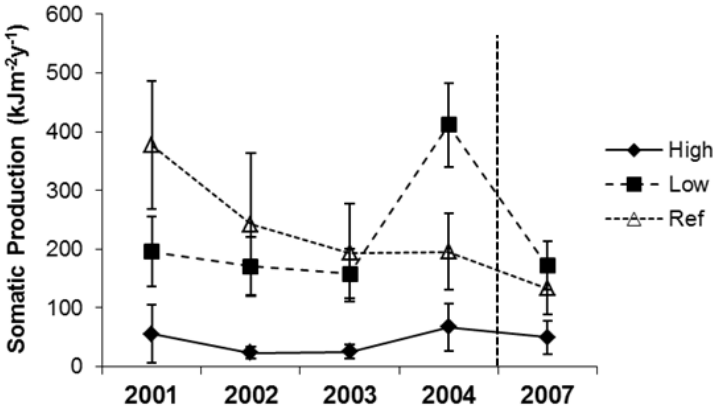

Figure 4.2. Summary of means and 95% confidence intervals of Somatic Production at sites of high and low dredging intensity and the reference site. The dotted vertical line indicates the discrepancy in time intervals.

Analysis by multivariate technique shows that samples from the low intensity and reference sites are more closely together than the samples from the high intensity site (Figure 4.3). ANOSIM results (Table 4.1) showed no significant difference in the level of production at the low intensity and reference sites in 2002 (i.e. 5 years after the cessation of dredging). No similarity was evident at the high dredging intensity site relative to the reference sites. The increasing similarity between both dredging sites and reference sites over the period of investigation, as shown by a decreasing ANOSIM R value, indicates that the energy transfer rate was starting to recover relative to the reference condition.

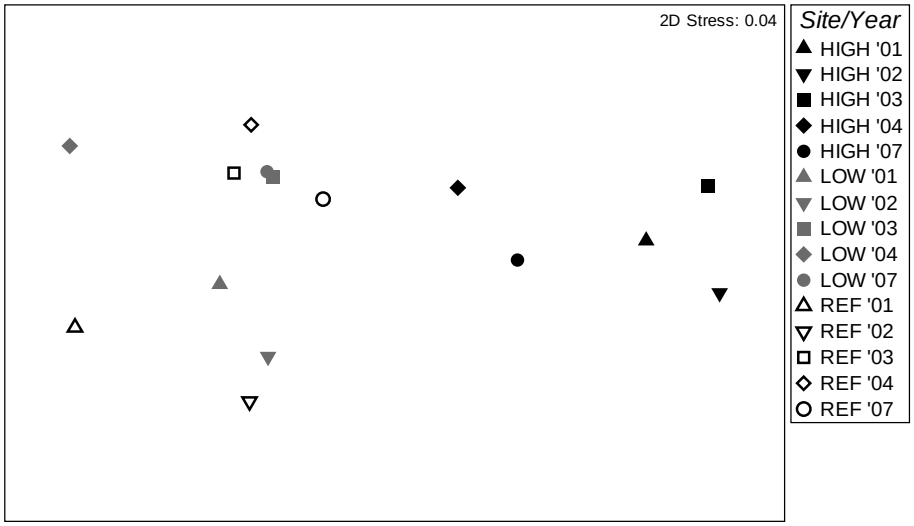

Figure 4.3. An MDS plot of Bray-Curtis similarity of Somatic Production at the high and low dredging intensity sites and reference site from 2001 to 2007.

Table 4.1: Summary of R-values derived from ANOSIM test based on values from Somatic Production (Ps),Infaunal Trophic Index and Biological Traits Analysis techniques.

Technique	High/Ref	Low/Ref
Ps		
2001	0.685**	0.164*
2002	0.742**	-0.005
2003	0.555**	0.025
2004	0.229**	0.282**
2007	0.145*	-0.030
ITI		
2001	0.843**	0.540**
2002	0.943**	0.284**
2003	0.882**	0.036
2004	0.410**	0.479**
2007	0.369**	0.282**
BTA		
2001	0.880**	0.533**
2002	0.953**	0.122*
2003	0.908**	0.002
2004	0.353**	0.581**
2007	0.385**	0.400**

* Significant difference at $p < 0.01$. ** Significant different at $p < 0.05$

4.3.2 Infaunal Trophic Index

Mean ITI values in 2001 to 2007 range from 62 to 84 (Figure 4.4). All mean values were greater than 60, which indicate that both dredging sites were at least in normal (or unaffected) condition throughout the study period. There were however several individual samples with values of less than 60. All of these samples were from the high intensity site, indicating a possible effect of dredging.

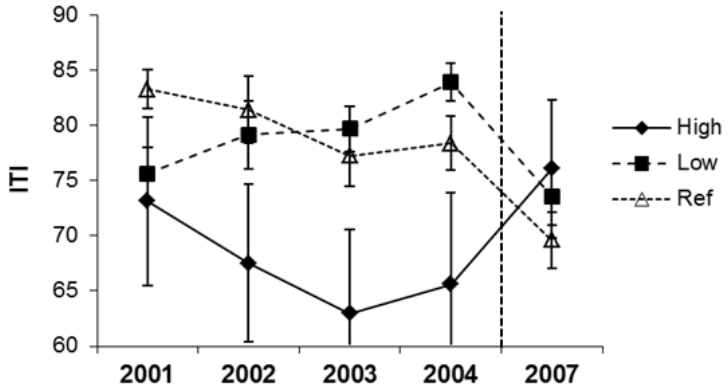

Figure 4.4. Yearly mean values (±95% confidence intervals) of Infaunal Trophic Index for high and low dredging intensity sites and reference sites. The dotted vertical line indicates the discrepancy in time intervals.

A multidimensional scaling (MDS) ordination revealed that dredging intensity was a major factor that changed the infaunal community, with samples from the high intensity site more widely dispersed than those of the low intensity and reference sites (Figure 4.5). This observation was confirmed by the results of ANOSIM test (Table 4.1) which revealed higher R values for the High/Reference comparison. Despite the generally more dispersed nature of the high intensity site's samples, the overlapping of sample from year 2007 with those from the reference sites showed that these assemblages had a similar functioning to those in undisturbed sediments.

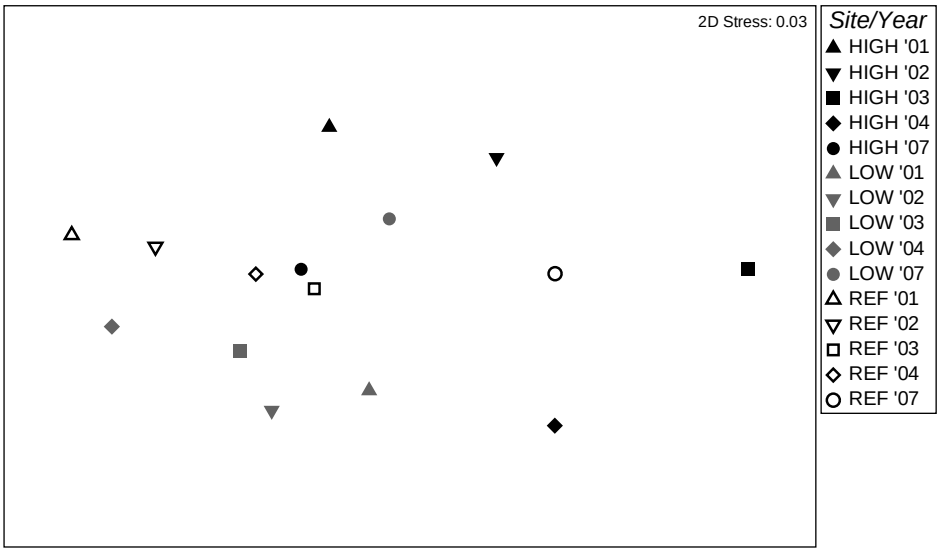

Figure 4.5. An MDS plot of Bray-Curtis similarity of Infaunal Trophic Index at the high and low dredging intensity sites and the reference sites from 2001 to 2007.

4.3.3 Biological Traits Analysis

Biological Traits Analysis (BTA) does not produce any numerically meaningful value to be compared using univariate statistics. For this reason, the trait-by-sample values arising from this technique were analysed using multivariate statistics to compare the dispersion of assemblages between sites (Figure 4.6). Samples from the low intensity site are closely grouped with the samples from the reference site, while sample of the high intensity site are distinctly spread to the opposite side. The functional traits of the community at the high intensity site were significantly different compared to the undisturbed site throughout the study period (Table 4.2). Meanwhile the assemblage at the low intensity site was functionally similar by 2003, although one year after that (2004) and in 2007 the biological functions of the assemblages differ from the reference site.

The counter-intuitive results in 2003, 2004 and 2007 from the low intensity site were further investigated using SIMPER analysis. This revealed that in those years, the top two traits that contributed the most to the dissimilarity between the two sites were LARVAL TYPE_planktonotroph and SIZE_1-3 cm. Further investigation through SIMPER analysis of abundance data revealed that the significantly high abundance of *Pomatoceros lamarcki* in 2004 and 2007 contributed to the functional difference in this site compared to the reference site. This polychaete worm, which has 100

percent affinity to the two traits, was the highest contributor to the dissimilarity between these sites in 2004 and 2007, but not in 2003 (Table 4.3).

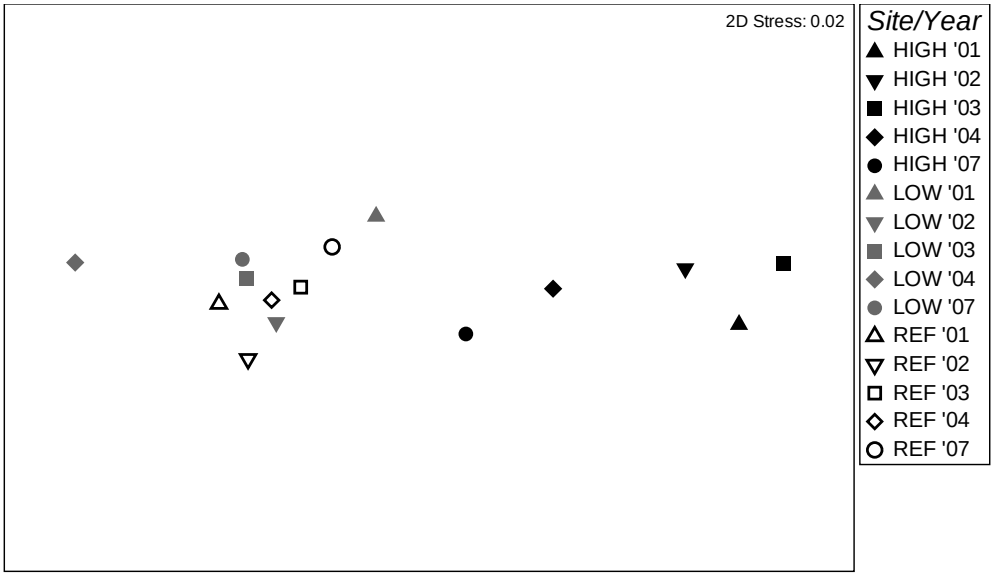

Figure 4.6. An MDS plot of Bray-Curtis similarity of BTA at the high and low dredging intensity sites and the reference site from 2001 to 2007.

Table 4.2. Results of SIMPER analysis of the traits that contribute to the dissimilarity between two samples. The pairings are between samples from Low and Reference sites from 2003 – 2007.

Groups LOW '03 & REF '03						
Trait	LOW '03 Av.Abund	REF '03 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Planktotroph	166.2	112.4	2.15	1.32	7.45	7.45
1-3cm	140.4	92.92	1.94	1.45	6.69	14.14
Low mobility	129.98	79.41	1.84	1.45	6.37	20.51
Short cylindric bodyform	124.42	75.96	1.79	1.51	6.19	26.7
Suspension/filter	132.37	92.35	1.78	1.41	6.16	32.86
None attachment	127.17	103.88	1.66	1.42	5.74	38.6
Tube - permanent attachment	103.63	57.47	1.64	1.5	5.68	44.28
Permanent attachment	115.65	80.75	1.62	1.38	5.6	49.88
Surface crawler	52.44	46.4	0.92	1.32	3.19	53.07
Burrower	73.48	58.98	0.86	1.36	2.98	56.05

Groups LOW '04 & REF '04						
Trait	LOW '04 Av.Abund	REF '04 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Planktotroph	405.65	134.5	4.72	2.29	10.71	10.71
1-3cm	310.23	95.11	3.65	2.09	8.3	19.01
Low mobility	290.37	93.78	3.41	2.25	7.75	26.77
Short cylindric bodyform	271.38	70.79	3.4	2.19	7.72	34.48
Suspension/filter	282.54	90.63	3.25	2.07	7.39	41.87
Permanent attachment	272.75	81.25	3.25	2.16	7.37	49.25
Tube - permanent attachment	242.92	51.95	3.22	2.26	7.31	56.56
None attachment	233.65	134.25	2.04	1.55	4.63	61.19
Gravel	131.85	47.45	1.47	2.08	3.33	64.52
Stone	124.3	47.93	1.34	2.01	3.04	67.57

Groups LOW '07 & REF '07						
Trait	LOW '07 Av.Abund	REF '07 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Planktotroph	158.6	78	2.26	1.7	8.03	8.03
1-3cm	124.87	52.73	2.06	2.03	7.32	15.35
Short cylindric bodyform	99.43	33.65	1.92	2.06	6.83	22.18
Tube - permanent attachment	80	16.46	1.84	2.14	6.53	28.71
Permanent attachment	127.95	67	1.8	1.64	6.4	35.11
Suspension/filter	113.73	52.61	1.78	1.96	6.32	41.43
Low mobility	116.68	70.66	1.51	1.56	5.37	46.8
None attachment	113.2	88.57	1.32	1.31	4.68	51.48
None mobility	66.83	43.23	0.88	1.35	3.14	54.62
Burrower	74.99	65.14	0.86	1.37	3.05	57.67

Table 4.3. Results of SIMPER analysis of the main characterising species that contribute to the dissimilarity between two samples. The pairings are between samples from Low and Reference sites from 2003 – 2007.

Groups LOW 03 & REF 03						
Species	LOW 03 Av.Abund	REF 03 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Anthura gracilis	0	1	0.76	2.5	1.45	1.45
Praxillella affinis	1.07	0.22	0.72	1.51	1.38	2.83
Pisidia longicornis	1.71	1.4	0.72	1.1	1.38	4.22
Notomastus	1.38	0.54	0.68	1.38	1.31	5.53
Verruca stroemia	0	0.86	0.63	0.92	1.21	6.75
Mysella bidentata	0.87	0.22	0.63	1.1	1.2	7.95
Ophiura (juv.)	1.83	1.11	0.61	1.05	1.17	9.12
Janira maculosa	0.38	0.86	0.59	1.22	1.14	10.26
Corophium sextonae	0.87	0.71	0.59	1.22	1.14	11.4
Cheirocratus	0.84	0.92	0.58	1.11	1.11	12.5

Groups LOW 04 & REF 04						
Species	LOW 04 Av.Abund	REF 04 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Pomatoceros lamarcki	3.61	2.18	0.79	2.1	1.63	1.63
Ophiura albida	1.33	0.1	0.7	1.93	1.43	3.06
Scalibregma inflatum	1.64	0.67	0.61	1.64	1.26	4.32
Ophiura (juv.)	2.36	1.36	0.6	1.2	1.22	5.54
Pomatoceros triqueter	1.44	0.43	0.57	1.66	1.17	6.71
Ampharete lindstroemi	1.19	0.4	0.53	1.58	1.09	7.8
Psammechinus miliaris	1.19	0.46	0.51	1.41	1.04	8.84
Sthenelais boa	0.97	0.12	0.5	2.06	1.02	9.86
Praxillella affinis	1.25	0.51	0.5	1.36	1.02	10.88
Pisidia longicornis	2.69	2.05	0.48	1.4	0.98	11.86

Groups LOW 07 & REF 07						
Species	LOW 07 Av.Abund	REF 07 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Pomatoceros lamarcki	2.73	1.6	0.69	1.97	1.42	1.42
Serpulidae	1.56	0.45	0.67	1.79	1.38	2.8
Gibbula tumida	0.92	0.22	0.51	1.34	1.05	3.85
Mysella bidentata	0.47	0.92	0.51	1.18	1.04	4.89
ACTINIARIA	1.45	1.5	0.5	1.21	1.03	5.92
Phoronis	0.84	0.8	0.48	1.27	1	6.92
Pomatoceros triqueter	0.96	0.4	0.48	1.34	1	7.91
Anthura gracilis	1.26	0.83	0.48	1.26	0.98	8.9
Pisidia longicornis	1.47	0.9	0.47	1.26	0.97	9.87
Ophiura albida	1.06	0.45	0.47	1.3	0.96	10.83

4.3.4 Rao's Quadratic Entropy

At the high dredging intensity site, the average value of Rao's Quadratic Entropy was generally lower than that recorded at the low intensity and reference sites (Figure 4.7). The only significant difference was recorded at the low intensity site in 2004 and the high intensity site in 2007 (one-way ANOVA: $p < 0.05$). This might be due to the strange property of this index where its value may decrease as a consequence of an increasing number of species (Botta-Dukat, 2005). The reason is that Rao's Q is influenced by both species-abundance based diversity and by trait differences among species. As in the case of the low intensity site in 2004 and at the high intensity site in 2007, high number of individuals had increased species-abundance based diversity, but at the same time it may decrease the average dissimilarity among species as the addition of new species did not proportionally add new traits into the system. The decrease of average dissimilarity means these sites have a high average similarity, and hence a smaller functional diversity (Botta-Dukat, 2005).

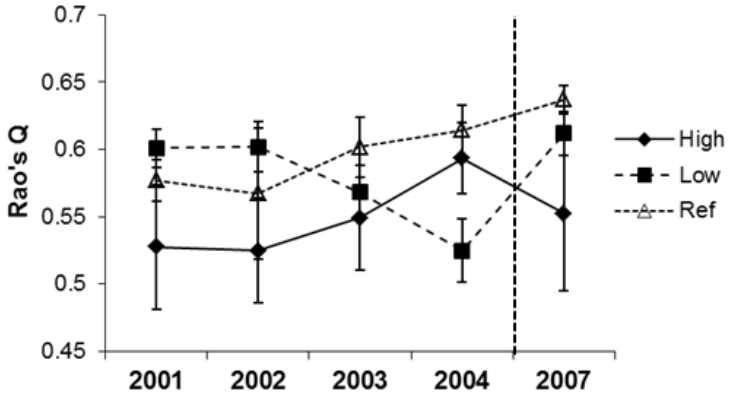

Figure 4.7. Yearly mean values (±95% confidence intervals) of Rao's Quadratic Entropy index at the high and low dredging intensity sites and the reference site. The dotted vertical line indicates the discrepancy in time intervals.

The MDS shows that samples from all sites are diffusely distributed as much as they clustered together (Figure 4.8). Similarly, samples from both dredged sites are also widely scattered from year to year. The ordination patterns of the MDS conform to the ANOSIM results which show no obvious patterns at either high or low intensity site over the period of study (Table 4.4).

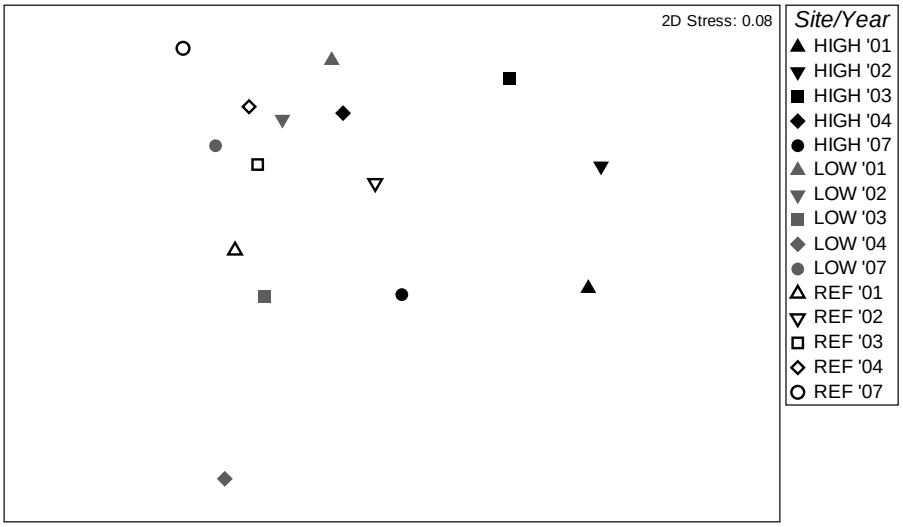

Figure 4.8. An MDS plot of Bray-Curtis similarity of Rao's Q at the high and low dredging intensity sites and the reference sites from 2001 to 2007.

Table 4.4: Summary of R-values derived from ANOSIM test based on values from Rao's Quadratic Entropy (Rao's Q) and Functional Diversity (FD).

Technique	High/Ref	Low/Ref
Rao's Q		
2001	0.397**	0.382**
2002	0.134*	0.049
2003	0.286*	0.190*
2004	0.043	0.662**
2007	0.147*	0.237**
FD		
2001	0.587**	0.060
2002	0.345**	0.041
2003	0.627**	-0.010
2004	0.423**	-0.064
2007	0.428**	0.039

* Significant difference at $p < 0.01$. ** Significant different at $p < 0.05$

4.3.5 Functional Diversity

The mean values of Functional Diversity at the high dredging intensity site were in general the lowest throughout the study period (Figure 4.9). Meanwhile, the low intensity site was functionally similar to the reference site where the mean values recorded no significant different (one-way ANOVA: $p > 0.05$). The effect of species richness and composition on FD is shown in Figure 4.10 with a linear relationship evident at all three sites. The plots show that the sites contained species that were complementary to each other. It means that the increase of FD as a result of the addition of any one species to the site was similar to the addition of any other species. The variation around the linear line for the reference site was more apparent

than for both dredging sites, indicating that species identity played a greater role in determining FD at the reference site.

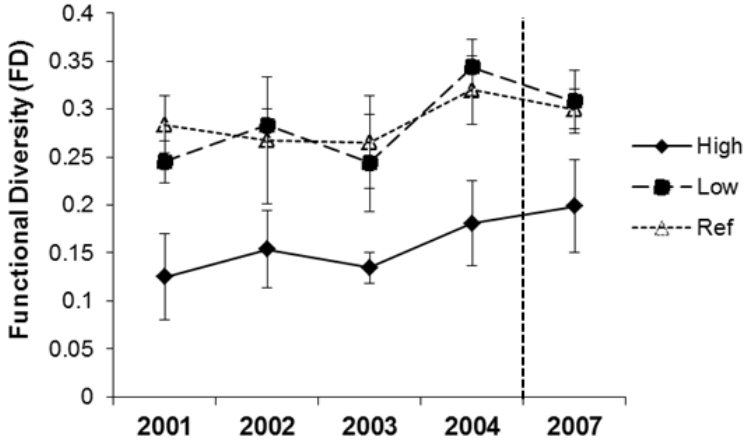

Figure 4.9. Yearly mean values (±95% confidence intervals) of Functional Diversity index at the high and low dredging intensity sites and the reference site. The dotted vertical line indicates the discrepancy in time intervals.

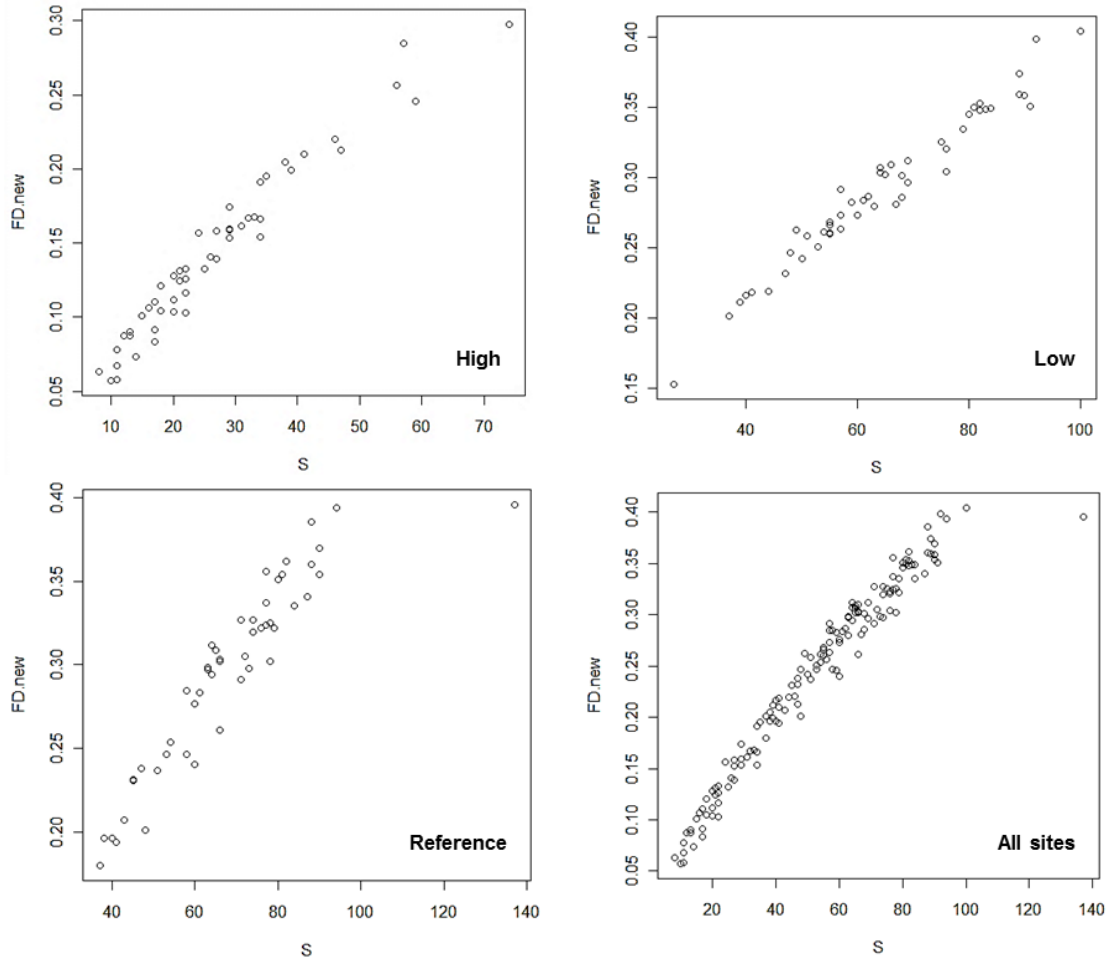

Figure 4.10. Effect of the number of species in determining the FD values at the high intensity, low intensity and reference sites, as well as a combination of all sites.

The MDS ordination shows that samples from the low intensity site had high similarity with samples from the reference site in terms of functional diversity (Figure 4.11). This is based on the overlapping of samples from these sites. In contrast, the more dispersed samples from the high intensity site indicates a lower similarity to the reference site. This trend is supported by the ANOSIM R values (Table 4.3) which show that the high site was significantly different ($p < 0.01$), while the low site was not different ($p > 0.05$) from the reference site.

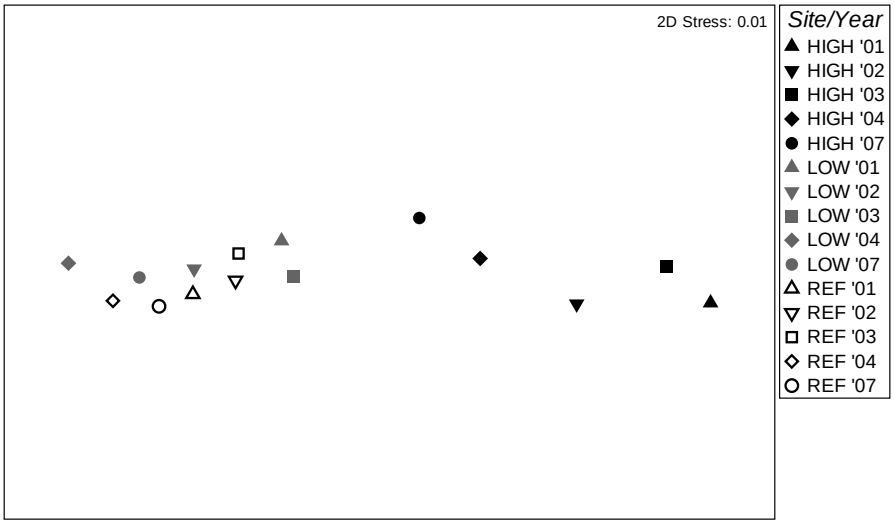

Figure 4.11. An MDS plot of Bray-Curtis similarity of FD at the high and low dredging intensity sites and the reference site from 2001 to 2007.

4.3.6 Predictive time of recovery at the high dredging intensity site

The prediction of full recovery at the high dredging intensity site is presented in Figure 4.12. With the exception of Ps, the predictive times for this site to functionally recover were fairly similar between exponential and linear fitting line. The fastest recovery time was predicted based on exponential Rao's Q and FD indices (~14.5 years). Meanwhile, the range of recovery based on linear fitting line was between 16 – 18 years. A substantially longer period of functional recovery was predicted using Ps with ~32 and ~68 years respectively based on exponential and linear lines.

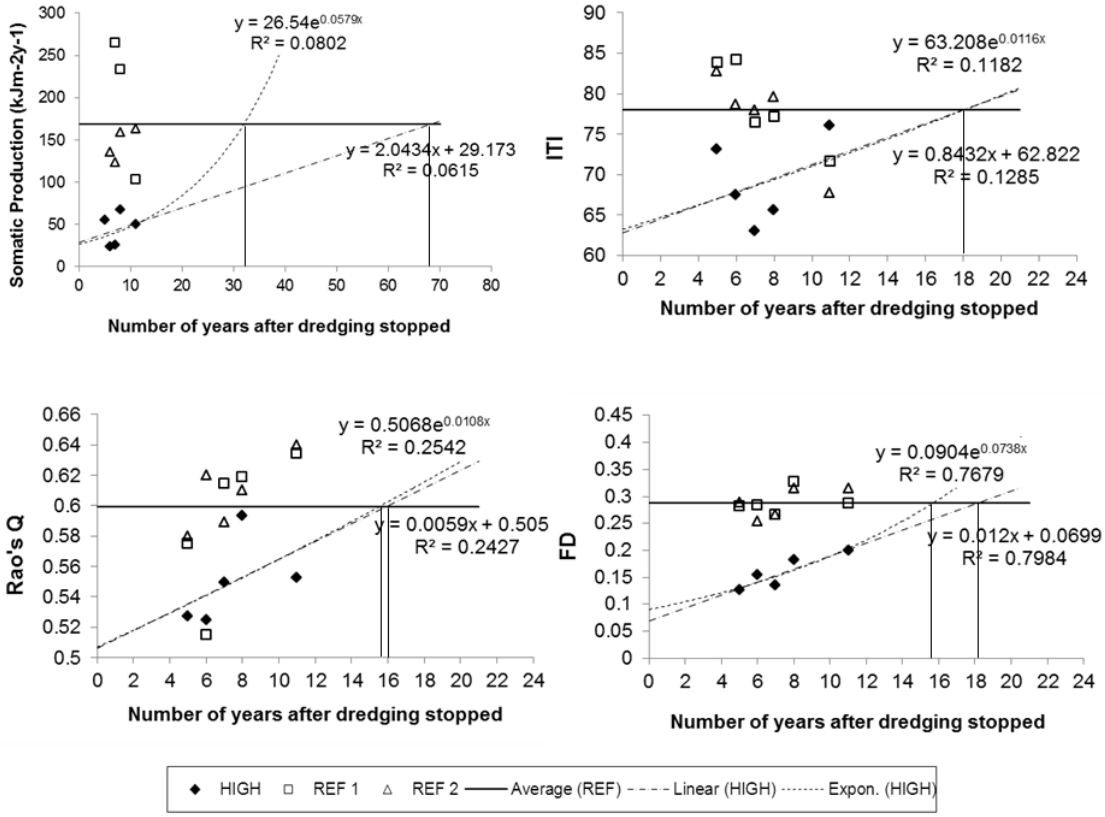

Figure 4.12. Trajectory of predictive time of macrofaunal recovery at the high intensity site based on different functional analyses.

4.4 Discussion

The communities observed at dredged sites had functionally changed especially when the intensity of disturbance was concerned. In addition, there were indications that the dredged sites were progressing toward recovery, or in certain cases had already recovered. Nevertheless, the recovery trend was not clear since the sites recorded variability in the functional values, although this variability was expected as the marine system is a dynamic environment that is continuously responding to many factors such as local hydrodynamic, community interaction and food availability. Besides the variability of the communities over time, the variability was also apparent in terms of the recovery period measured by different indices.

4.4.1 Recovery based on different indices

Generally, annelids and crustaceans were the taxa with the highest production value throughout the study period. The life history pattern of these groups is assumed to contribute to this trend. High agility and motility exhibited by most annelids and

crustaceans might contribute to more efficient food capture than molluscs and echinoderms which have lower agility and motility (Brey and Clarke, 1993). However, it is also worth taking into consideration that the high production value possessed by annelids and crustaceans in this study was due to their natural dominance at Area 222. The total somatic production of the assemblages is determined by processes such as reproduction, growth and mortality which collectively occur at community level (Sarda et al., 2000). Somatic production is also affected by emigration of large-bodied fauna and continuous recruitment (Pombo et al., 2007). For instance, physical damage at dredging sites may lead many original inhabitants to migrate to other areas, and then after several years, a new set of recruits moved into the dredging sites. Both the migration and recruitment may decrease the mean individual size and weight, hence the negative growth of the system. In the present study, the effect of physical activity which subsequently changes migration, dispersal and aggregation patterns of the community was shown at the high dredging intensity site. In contrast to the low intensity site, samples from the high intensity site were less similar to the reference site, suggesting that dredging intensity had reduced the energy transfer among the macrofaunal community, subsequently limiting their growth (i.e. biomass). Apart from biological interaction, it is believed the reduction of the food source at the high intensity site (as a consequence of intense dredging) might be have impeded the biomass growth of the communities, and therefore the whole production (Wootton, 1986). Effects of body size and function were considered in Appendix 1.

The Infaunal Trophic Index indicates feeding mechanisms of benthic infauna. The index values also implicitly correspond to the amount of particulate matter present in the sediments and in the water column (Word, 1979). For instance, the dominance of deposit feeders reflects the increased amounts of particulate matter. The ITI value is also strongly influenced by the variability of species abundance (Maurer et al., 1999). This relationship is shown in the present study. For instance, the high intensity site with the lowest macrofaunal abundance was represented by the lowest ITI value. The converse also occurred at the low intensity site with higher abundance and higher ITI values. The ITI value was also strongly influenced by certain groups (in this case it was Group 1). This was observed as the high intensity site with the lowest proportion of Group 1 infauna (suspension feeder) resulting in the lowest ITI in 2003, while the low intensity and reference sites, which comprised of higher proportion of this group, had higher ITI values. This changed in 2007, when the proportion of Group 1 at the

high intensity site was the highest compared to the other sites, and as a result, the ITI value was also highest at this site. According to Levinton (1991), the distinction between feeding groups of fauna can be distorted by the high numbers of opportunistic species. Therefore, it can be argued that the highest ITI value recorded at the high intensity site in 2007 was actually caused by the high abundance of opportunistic species rather than the proportion of the groups.

Biological traits composition varied between sites with the variation increased as dredging intensity increased. The impact of physical disturbance on biological traits accords with other studies (fishing intensity) in the southern North Sea and eastern English Channel (Bremner et al., 2003). The life history traits, in particular 'Planktotroph' was found to be the major trait that determined the dissimilarity between dredged and undisturbed sites. Planktotrophic larval development is common in marine benthic fauna, especially polychaetes, and their larva are characterised by a high level of production and a high potential for dispersal over long distances (Strathmann et al., 2002). However, as the difference between dredged and undisturbed sites in terms of planktotrophic species was notable, it is assumed that the recruitment of this species to dredged sites was not that successful. This might due to the fact that these larva also have a high mortality rate because they spend a long time in the water column (Roughgarden et al., 1985; Caley et al., 1996).

By combining several traits, Rao's Q shows that factors affecting ecosystem function were not exclusively dependent on species composition and diversity. Diversity of functional traits appeared to be another aspect that could change the ecosystem. The univariate measure of Rao's Q in the present study showed that the impact of dredging was less obvious as the dredged sites showed a high degree of similarity with the reference site. This result is consistent with the theory suggesting the range and value of functional traits are important determinants that determine ecosystem function (Tilman et al., 1997; Hector et al., 1999). The univariate analysis also revealed that both dredged sites had already recovered in terms of functional diversity at the outset of the study. However, this finding should be treated with caution as dissimilarities between sites were still obvious in multivariate analysis, which could lead to assumption that no recovery has occurred. There are three factors that determine Rao's quadratic entropy, namely species diversity, species distinctness and abundance. Of these factors, only abundance was affected by the

correlation among traits. This might also explain the strange property recorded for the Rao's value in present study.

Assessing ecosystem function using FD shows that the recovery at the high intensity site has yet to take place whereas the site with lower dredging intensity has already recovered. This index also recorded a strong correlation between traits diversity and species richness. This relationship shows that the species' traits in Area 222 were equally complementary (Sala et al., 1996; Tilman et al., 1997; Diaz and Cabido, 2001; Petchey and Gaston, 2002). Petchey and Gaston (2002) pointed out that factors such as number of traits and how the traits are weighted influenced the effective dimensionality of trait space, and thus the relative important of species richness on FD. High number of effective trait dimensions leads to a decrease of the relative importance of species richness. The use of multiple traits and weighting the traits equally should decrease the importance of species richness. However, the converse was recorded in the present study. A possible explanation is because Area 222 was inhabited by a high abundance of rare species which are functionally different from each other. The addition of these species to the system will increase the FD proportionally without reaching asymptote that would reduce the importance of species richness. However, the asymptote would theoretically be reached if the samples were collected from a bigger pool.

The period of time needed for system recovery varies depending on the method of assessment used (Table 4.5). According to Rao's Q, the recovery at the high intensity site took place in 2004, eight years after cessation of dredging. However, the recovery was not apparent even in the last year of the study (11 years after dredging stopped) based on Ps, BTA and FD. The difference between the high intensity and reference sites was also still apparent in 2007, suggesting no recovery took place. However, as the mean ITI score was above the 60 threshold at all sites, this suggests the high intensity site had already classified as unaffected area since 2001 or before. The recovery time at the low intensity site suggested by all indices was earlier than the site with higher dredging intensity and had taken place during the period of the study. Rao's Q and FD suggested the fastest recovery, while the slowest recovery was suggested by ITI and BTA indices. Although there are discrepancies of the suggested recovery times, all indices were at least able to distinguish the impact of ecosystem function due to different intensity of dredging.

Table 4.5. Recovery times at the High and Low dredging intensity sites based on univariate measure of functional analyses.

Index	Year of recovery (Number of year after dredging)	
	Low site	High site
Somatic Production (Ps)	2002 (6)	> 2007 (> 11)
Infaunal Trophic Index (ITI)	2003 (7)	> 2007 (> 11)
Biological Traits Analysis (BTA)	2003 (7)	> 2007 (> 11)
Rao's Quadratic Entropy (Rao's Q)	≤ 2001 (≤ 5)	2004 (8)
Functional Diversity (FD)	≤ 2001 (≤ 5)	> 2007 (> 11)

4.4.2 Index performance and limitations

Ps is highly relevant to understanding ecosystem function (Pombo et al., 2007) as it is related to characteristics such as biomass and density, life span, recruitment, taxonomy and trophic status (Cusson, 2005). As pointed out by Cusson (2005), different taxa, functional traits and habitats have an important influence which determines the annual production of benthic organisms. In reference to the taxa, different individual species within a family may exhibit different characteristics which influence different rates of production. However, as conversion factors for production are currently only available at the family level there is a potential that the value of production was not accurately presented. For this reason it has to be treated with caution in assuming that there are indeed no differences in production between the sites in the present study. Furthermore, as mentioned earlier, the migration and recruitment of the organisms may cause inaccuracy in determining somatic production. This is rather difficult in the context of the present study because as the sites were undergoing recovery and recolonisation processes, the loss of some individuals together with the addition of others is normal.

Another biological characteristic, feeding behaviour, which is the central process in an ecosystem, is used as the basis for the ITI. Intrinsically, feeding behaviour can be used to measure the community response to organic materials. For example, an increased amount of sediment particulate matter may be related to the dominance of deposit feeding infauna (Maurer et al., 1999). The drawback of this index is due to its focus only on feeding behaviour. As a result, the ITI may ignore other ecological functions that are important in structuring ecosystems (Charvet et al., 1998; Mancinelli et al., 1998) and therefore be less sensitive in detecting changes in ecosystems. Some studies also suggest that feeding mechanisms may not always change following disturbance (Ramsay et al., 1998; Jennings et al., 2001). The score system to classify the status of ecosystems also seems less sensitive. In this study,

although there were times where the sites had significantly lower value than the undisturbed site, the ITI score suggested that all sites (and every year) were at least in ‘normal’ condition. However, it is worth bearing in mind that the less sensitive attribute might be due to the fact that the ITI was originally developed to assess organic enrichment rather than physical disturbance. This scoring system also could create a debate as to whether the system should be as similar to the undisturbed condition as the benchmark of recovery, or a certain threshold below the value of natural condition could be accepted when classifying recovery status. The other limitation of the ITI is its scaling factors are weighted towards groups 3 and 4 (deposit feeders) as the main purpose of this index is to measure the sensitivity of infauna towards organic matter (Maurer et al., 1999). This undermines the influence of other ecological changes on the infauna.

BTA has an advantage for determining ecosystem function because this index uses multiple functional traits. As the traits reflect the responses of every species to habitat constraints, the BTA is useful to show the link between organisms and the environment (Bremner et al., 2003). However, there are limitations of this metric that need to be taken into account. Given there is a wide range of traits available, selection of a few most important and meaningful traits can be problematic. Likewise, dismissing certain traits could give false interpretation on describing the relationship within assemblages, especially if the traits have the biggest influence on the whole community (Bremner et al., 2006). The mathematical analysis which is constrained to only multivariate technique makes this index difficult to be interpreted depending on different approaches (Bremner et al., 2003). This complexity will then affect the dissemination of the assessment to a wider target.

The same considerations of the (dis)advantages of multiple traits should also be given if Rao’s Q were to be selected. However Rao’s Q seems to be more detailed as it measures the pair-wise dissimilarity between every species in a sample, compared to BTA that simply sums up the traits values of all species in the sample. Different methods of measuring the pair-wise distance have also been used in many studies (e.g. Rao, 1982; Champely and Chessel, 2002; Rodrigues and Gaston, 2002). In spite of its simplicity, the pair-wise distance method could have a mathematical problem. In theory, when a species is added to a community, functional diversity should increase if the species functionally different from those already present (or

should be unchanged if the newly added species is functionally similar). In contrast, addition of a new species can decrease the mean of the pair-wise distance if the species is less different than the other species already in the system. For example, in a 4 species community which has a complete different functionality (i.e. no single traits are shared between species), the addition of another species which in some way has similarity with some of the functions of the other 4 species will disproportionately increase the total pair-wise distance, while decreasing the mean of the distance (Petchey and Gaston, 2006). As mentioned above, great care should be given to the results of this technique given its unexpected property where values may decrease if species richness increases. However, this downside might be mitigated when comparing this index at a large spatial scale given the fact that speciose communities normally correspond to high abundance and high diversity taxa (Péru and Dolédec, 2010). Therefore this unexpected property could be avoided as the increase of abundance is proportional to the increase of species richness.

FD is another index using a combination of multiple traits; hence it also warrants consideration with regards to the problems in dealing with the traits selection. In addition, this index also has a close resemblance to Rao's Q as it measures the functional diversity using the pair-wise distance method. The only difference is that FD does not include the number of individuals (evenness) in the calculation. While it proved to be a problem in Rao's index, the inclusion of the evenness aspect to measure functional diversity is intuitively appealing, as is the case with the inclusion of evenness in measuring species diversity (e.g. Simpson index). Mouillot et al. (2005) argued that a community with, say, 10 individuals with different traits values is more diverse than a community with the same number of individuals but majority of them exhibit the same traits value. The importance of incorporating the evenness is shown in several theoretical models and experimental works (Nijs and Roy, 2000; Polley et al., 2003; Dangles and Malmqvist, 2004). The other limitation shown by FD is its highly dependence on species richness, which in a way hinder the importance of different functional traits in measuring ecosystem function.

The trajectory of full recovery at the high intensity site showed some degree of similarity among different functional analyses where the indices recorded a prediction ranging from 14 to 18 years. The only obvious difference was the prediction using Ps where the full functional recovery is believed to take place over a much longer time.

Since the calculation of Ps is highly dependent on biomass, extra care should be taken when making inference of the recovery using this index (see section 3.4.5). However, for management purposes, the prediction using FD should be taken into account since it produced the highest confidence (i.e. the highest R^2 value).

4.5 Conclusion

In this study, five functional diversity indices which are suitable to be used with the nature of the dataset were tested. The results suggest that the different dredging intensities caused different level of changes in functional diversity. The use of different indices also produced different values for determining the recovery status. With the exception of Rao's Q, all indices suggest that additional works need to be done to determine the definitive time of recovery at the site with high dredging intensity. On the other hand, all indices suggest some recovery at the low dredging intensity site took place prior to, or at least during the period of the study. A prediction of recovery using univariate measure showed consistent findings where different indices suggested a fairly similar time for recover (except the Ps). Clearly, the results also suggest that in the context of this study, there was no single index that has definite advantage to the others. Although some indices take into account various biological and ecological factors in the measurement, the method of calculation make all indices suffer some limitations. For managerial purposes, it is impractical to use all the indices to determine the recovery of an area after disturbance. Therefore the index selection should reflect the purpose of study. The use of Ps in a study may be useful to assess the potential availability of food resources (e.g. for the fishing industry), as these indices are based on the body size of the macrofauna. ITI, which focuses exclusively on feeding guilds, could be used to determine the change of organic enrichment in a system. Indices using multiple traits (BTA, Rao's and FD) could be suitable in assessing habitat restoration, or in measuring the response of a community to different ecological changes. This does however require some expert knowledge on the part of the managers.

Declaration

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Chapter 5: Effects of changes in sediment characteristics for the structure and function of the macrofaunal community

5.1 Introduction

Marine aggregate dredging contributes to changes in the seabed environment in a variety of different ways. For example, through the creation of dredge furrows or pits (Kenny and Rees, 1996; Newell et al., 1998; Desprez, 2000; Boyd et al., 2004; Cooper et al., 2005; Cooper et al., 2007), changes to the local hydrodynamic regime through seabed deepening (Black et al., 2006), and the removal of sediment and alteration to its composition (Newell et al., 1998; Desprez, 2000; Boyd et al., 2005). Other effects include changes to the regional sediment transport regime through interception of sand, changes in the nature and stability of sediments accompanying surface screening or the exposure of underlying strata, and the increase of turbidity following the re-distribution of finer particles (Black et al., 2006). Changes in sediment composition draws considerable attention in aggregate dredging studies and they can happen in four ways: 1) the infilling of fine sediment into dredge tracks due to tidal currents; 2) the exposure of underlying sediments; 3) the return of fine sediments lost through overspill chutes during the loading of the cargo; 4) screening activity which returns unwanted sediments to the seabed (Newell et al., 1998; Cooper et al., 2007).

Changes in sediment composition due to dredging activity may lead to a change in the community that differs to the original assemblages (Desprez, 2000; Boyd et al., 2005; Cooper et al., 2011). A strong relationship between the composition of sediments and macrofaunal communities has been reported in coastal areas including the Irish Sea (Hensley, 1996), the Bristol Channel (Warwick and Davies, 1977) and the English Channel (Parry et al., 1999). Other studies in sheltered areas and deep waters in the North Sea and elsewhere also found this relationship (Dankers and Buekema, 1981; Künitzer et al., 1992; Mackie et al., 1995; van Dalfsen et al., 2000). There were a number of studies that found little correlation between these factors (e.g. Duineveld and van Noort, 1990; Kenny, 1998; Seiderer and Newell, 1999; Newell et al., 2001; Cooper et al., 2007) suggesting that the changes in biotic structure were not only caused by the sediment composition, but also other physical factors such as depth of disturbance by tidal scour and the strength of the currents (Holme and Wilson, 1985; Newell et al., 1998). In addition, the community

structure of the macrofauna is also dependent on processes at the sediment-water interface involving physical and biological factors such as changes in organic matter content, microbial abundance and composition, larval supply and particulate flux (Snelgrove and Butman, 1994).

The extent to which dredging activity affects sediment characteristics depends on the depth of the areas. Disturbance of gravel-sized particles due to tidal currents is commonly associated with the areas of less than 30 m depth. In contrast, disturbance by the currents in deeper areas is generally limited to fine particles (Seiderer and Newell, 1999). Areas characterised by gravelly sediments tend to be more affected by deposition of fine sediments (resulting from screening and overspill) than the areas characterised by mobile sands. This is because the gravel dominated areas are commonly inhabited by encrusting epifaunal species which have a lower resilience to disturbance in comparison to faunal communities found in mobile sands environments which normally are highly resilient (Desprez, 2000; Boyd and Rees, 2003). In addition, a recent study in dredged sites in the south and southeast coastal region of the UK reported that the areas dominated by gravel deposits were more likely to suffer changes in macrofaunal community structure and function (Cooper et al., 2011).

Hypothetically, with depth ranging between 27 m and 35 m, and naturally characterised by gravel deposits, the seabed at Area 222 is generally perceived as moderately sensitive to disturbance (Cooper et al., 2011). This study aims to examine the extent to which changes in sediment characteristics have occurred in areas of relatively high and low dredging intensity, and how these changes have influenced the structure and function of associated macrofaunal communities. Of particular interest, this study also examines how the return to dominance by the gravel fraction contributes towards the recovery of macrofaunal community. A requirement of government policy is that the seabed should be left in a similar physical condition post dredging (DCLG, 2002). Therefore, an improved understanding of the relationship between environment and biotic aspects will help in determining the best way in restoring the impacted environments.

5.2 Methods

5.2.1 Sediment statistical analysis

The textural class classifications which represent the percentage of gravel, sand and silt/clay fractions were made based on Brown and McLaachlan (1990) and are presented (Table 5.1).

Table 5.1. Classification of particle size

Particle Size	Diameter
Gravel	2.0 – 4.0 mm
Coarse sand	0.5 – 1.9 mm
Medium sand	250 – 499 µm
Fine sand	63 – 249 µm
Silt/clay	< 63 µm

Sediment sorting, which indicates the distribution of the grain sizes, was classified based on Dyer's (1985) nomenclature (Table 5.2).

Table 5.2. Classification of sorting

Type of sorting	Range
Very well-sorted	< 0.35
Well-sorted	0.35– 0.70
Moderately-sorted	0.70 – 1.00
Poorly-sorted	1.00 – 2.00
Very poorly-sorted	> 2.00

Skewness measures the shape of the particle size distribution (i.e. whether the curve has an asymmetrical tail towards the coarse or fine particle region) (Folk 1974). Skewness classification is presented (Table 5.3).

Table 5.3. Classification of skewness.

Type of skewness	Range
Very negative skew	-1.00 to -0.30
Negative skew	-0.30 to -0.10
Asymmetric skew	-0.10 to 0.10
Positive skew	0.10 to 0.30
Very positive skew	0.30 to 1.00

Kurtosis measures the shape of particle size distribution whether relatively flat or peaked in form. Classification of the kurtosis (McBride, 1971) is presented (Table 5.4): where mesokurtic approximates to a normal distribution.

Table 5.4. Classification of kurtosis.

Type of sorting	Range
Very platikurtic	< 0.67
Platikurtic	0.67 to 0.90
Mesokurtic	0.90 to 1.11
Leptokurtic	1.11 to 1.50
Very leptokurtic	> 1.50

The formulae for calculating mean, sorting, skewness and kurtosis are given (Table 5.5.). The percentile measure, ϕ_n, is the grain size in phi units at the *n*th percentage frequency (Ahmad, 1990; Tucker, 2001).

Table 5.5. Formula for calculating mean, sorting, skewness and kurtosis of the sediment.

Parameters	Formula
Mean	$= \frac{\phi_{16} + \phi_{50} + \phi_{84}}{3}$
Sorting	$= \frac{\phi_{84} - \phi_{16}}{4} + \frac{\phi_{95} - \phi_{5}}{6.6}$
Skewness	$= \frac{\phi_{16} + \phi_{84} - 2\phi_{50}}{2(\phi_{84} - \phi_{16})} + \frac{\phi_{5} + \phi_{95} - 2\phi_{50}}{2(\phi_{95} - \phi_{5})}$
Kurtosis	$= \frac{\phi_{95} - \phi_{5}}{2.44(\phi_{75} - \phi_{25})}$

5.3 Results

5.3.1 Sediment classification

Comparison of the sediment particle size characteristics of samples taken from Area 222 revealed differences between treatments over the period of study (see Table 5.6). For example, samples from the high dredging intensity site were better sorted than those of both the low intensity and reference sites (One-Way ANOVA; $p < 0.05$). Although differences remained in 2007, sorting values have showed a steady increase over the period of study. The higher sorting value (poorly sorted) of the sediment at the low intensity and reference sites can be explained by the higher

percentage of gravel which make the sediment composition highly variable. Sediments in Area 222 were generally highly positively skewed, indicating the distribution was characterised by a mode of coarser sediments with a large tail of excess fine sediments (Allen, 1985). However, skewness values at the high intensity site were notably lower ($p < 0.05$) compared to the values at low intensity and reference sites, especially in 2002 when a negative value was recorded (-0.02±0.71) that indicated this site was characterised by a mode of finer sediments. The values became less dissimilar in 2004 with 0.55±0.90, 0.59±0.24 and 0.62±0.57 skewness at the high and low dredging intensity and reference sites respectively. Meanwhile, kurtosis values at all sites in the entire period of study indicated that the sediments were very leptokurtic. Higher kurtosis values indicate a greater dominance of one particle size while the lower value indicates a more balanced distribution. According to Coleman et al., 2011, large positive values (as recorded at the high intensity site in 2001) can be related to the patchiness of sand waves on an otherwise flat bed.

Table 5.6. Mean values (±SD) of sediment particle size characteristics from samples collected at Area 222.

Year	Site	Mean particle (mm)	Sorting	Skewness	Kurtosis
2001	High	1.41(±1.07)	1.83(±1.22)	0.54(±0.79)	12.87(±10.12)
	Low	2.05(±0.83)	3.27(±0.44)	0.88(±0.36)	3.70(±0.40)
	Ref	1.57(±1.16)	3.59(±0.72)	0.90(±0.31)	3.74(±1.56)
2002	High	1.16(±0.47)	1.93(±0.96)	-0.02(±0.71)	6.20(±3.96)
	Low	1.23(±0.73)	3.44(±0.56)	0.58(±0.25)	2.97(±0.71)
	Ref	1.30(±1.34)	4.17(±0.93)	0.54(±0.62)	2.67(±1.34)
2003	High	1.89(±0.98)	2.35(±0.97)	0.13(±0.97)	4.29(±2.84)
	Low	1.35(±0.28)	3.41(±0.36)	0.71(±0.20)	3.11(±0.28)
	Ref	1.61(±2.08)	4.03(±0.75)	0.60(±0.72)	2.92(±1.69)
2004	High	2.36(±1.62)	2.59(±1.15)	0.55(±0.90)	4.74(±3.30)
	Low	1.25(±0.64)	3.60(±0.70)	0.59(±0.24)	2.73(±0.64)
	Ref	1.64(±1.76)	4.19(±0.81)	0.62(±0.57)	2.62(±1.28)
2007	High	1.95(±1.15)	2.98(±0.56)	0.26(±0.97)	2.80(±0.57)
	Low	1.13(±0.43)	3.30(±0.71)	0.33(±0.14)	2.39(±0.45)
	Ref	1.94(±2.11)	3.79(±0.50)	0.58(±0.42)	2.57(±0.72)

5.3.2 Inter-relations between statistical parameters

The relationship between the statistical parameters varies between very weak to modest positive correlations (Figure 5.1). The only negative correlation recorded was between mean grain size and sorting (r = -0.11). Sediments become more poorly sorted as they become coarser, until reaching the threshold of approximately 1.8 mm where the grain size did not have a strong influence on sorting type. Mean grain size recorded the strongest correlation with skewness (r = 0.57). There was a general trend of increasingly positive skewness with increasing mean grain size (Figure 5.1). Maximum skewness values were reached near the maximum mean grain size. Mean grain size shows a very weak correlation with kurtosis (r = 0.07). However, the relationship between these parameters was linear, where the increase mean grain size was associated with increasing kurtosis. Several plots representing a mean grain size of approximately 0.6 – 1.1 mm appeared to be associated with very high kurtosis values. This strange feature was due to the very high percentage of gravel recorded within several replicate samples from the high intensity site.

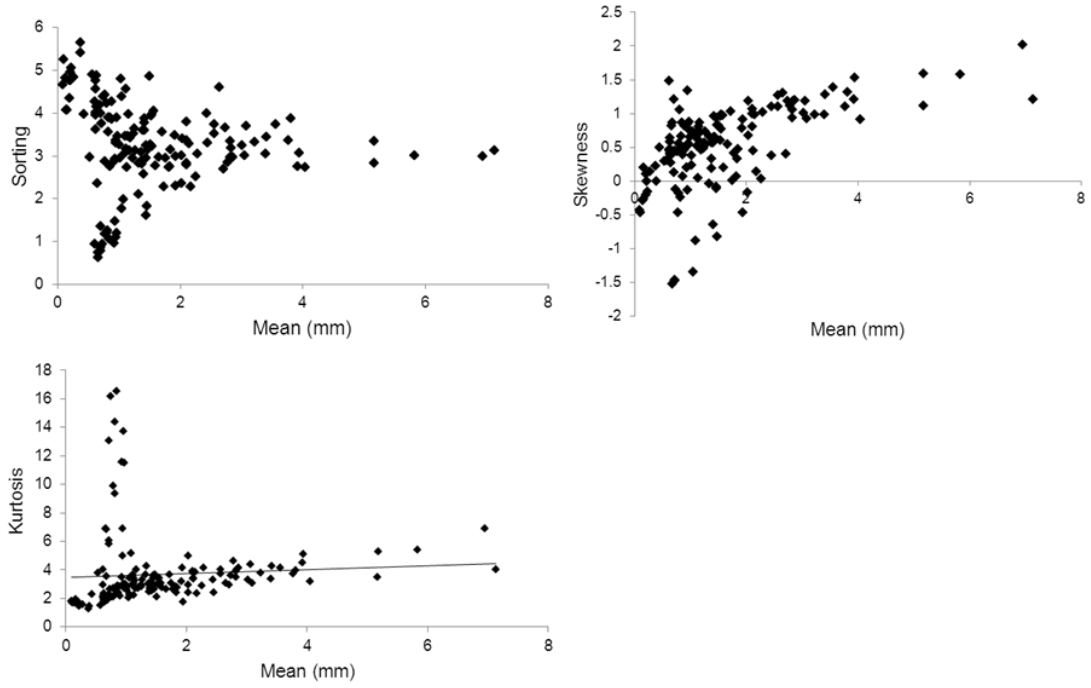

Figure 5.1. The relationship of mean grain size with the values of sorting, skewness and kurtosis of all sites over the whole period of the study.

5.3.3 Particle size composition

In terms of particle size, sediment samples at the low dredging intensity and reference sites were more similar to each other than to the sediments at the high intensity site (Figure 5.2). Generally, the low intensity and reference sites comprised around 44 - 58% of gravel. Although both sites were generally dominated by gravel, the composition of other sediment fractions differed between sites. The reference site was characterised by higher proportions of silt/clay and less medium sand than the low intensity site. The composition of the sediments from the reference site was also more variable. In contrast, sediment composition at the high intensity site was highly variable, particularly in terms of the gravel and sand fractions. Sediment samples contained proportionally less gravel (around 25-45%) and more coarse sand. However, toward the end of this study in 2007, samples from the high intensity site had changed and became similar to the other sites. This was due to the increase in the proportion of gravel and a corresponding decrease in the proportion of coarse sand over time.

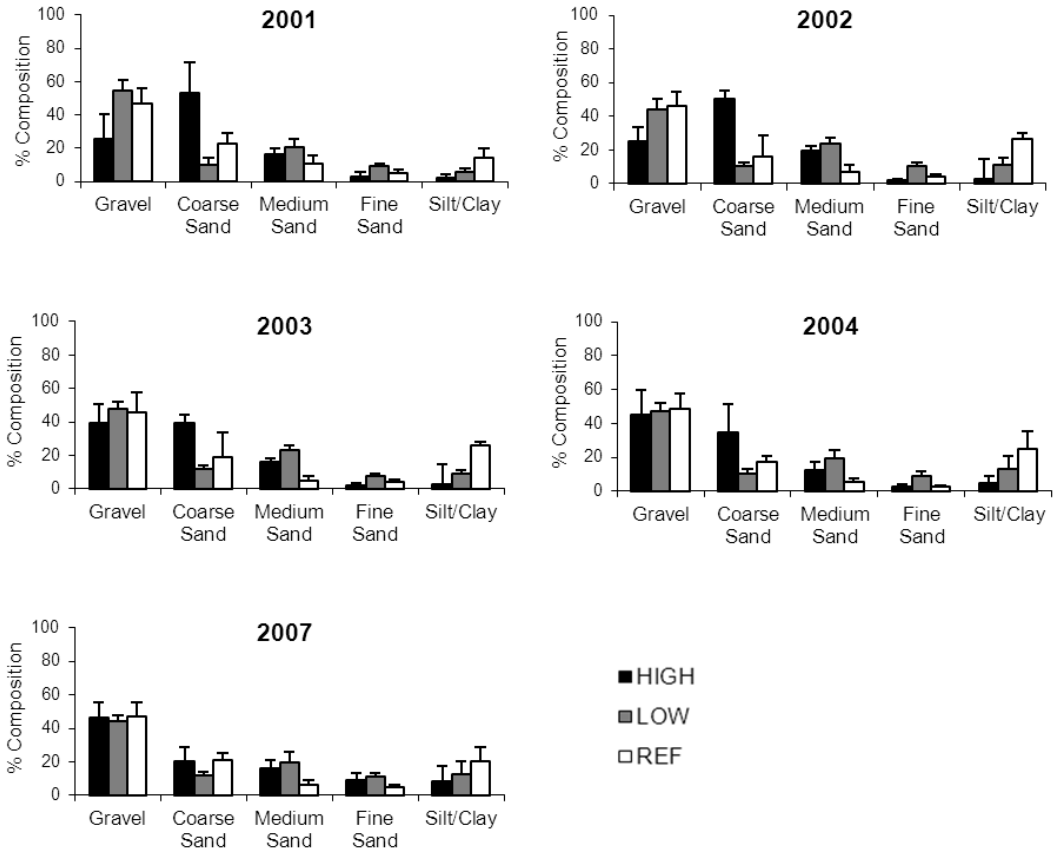

Figure 5.2. Mean particle size (± confidence intervals) of samples at the high and low dredging intensity sites and reference site from 2001 to 2004 and in 2007.

The difference of sediment composition between sites was reflected by the separation of the samples in the PCA ordination (Figure 5.3). The ordination is represented on two principle components (variable spaces) with the two axes accounting for 87% of the total variability within the data. The high variability indicates that these two principle components are suitable to show the similarity between sediments (Clarke and Gorley, 2006). The PCA shows the samples from the low intensity and reference sites are fairly closely together indicating a higher similarity in terms of particle size composition compared to the high intensity site. Although both sites were characterised by gravel, the low intensity site appeared to be dominated by silt/clay while fine sand was dominant at the low intensity site. In contrast, sediment composition at the high intensity site was dominated by medium and coarse sand. Over the period of study, samples from the high intensity (year 2007) site are increasingly comparable with samples from the low intensity and reference sites, indicating a trend of increasing sediment composition similarity.

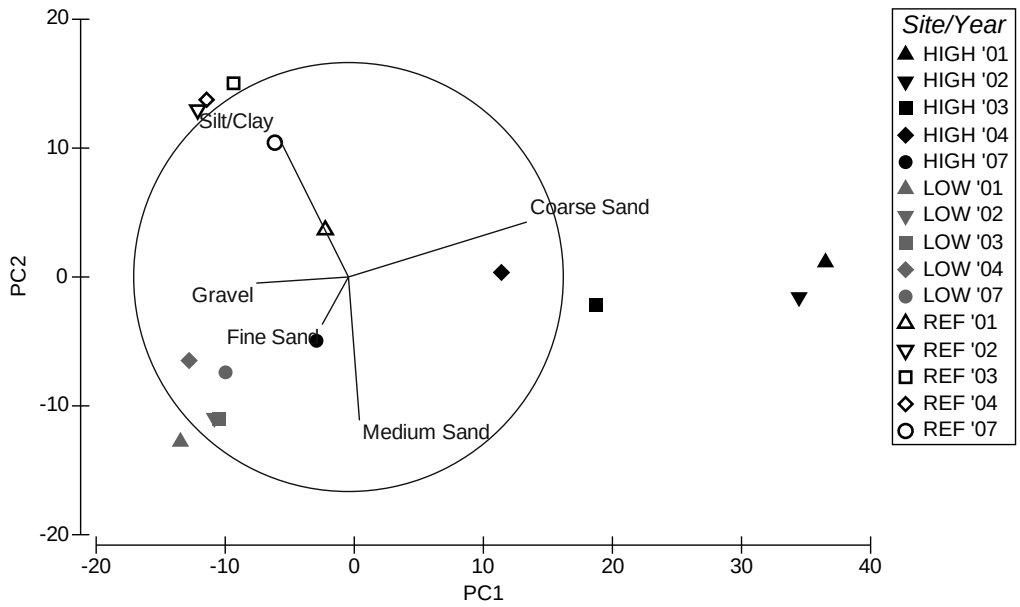

Figure 5.3. Two dimensional correlation-based PCA ordination of sediment particle size data from Area 222.

The separation of samples in the PCA ordination was confirmed by analysis of similarity (ANOSIM) R values which showed that both the dredging sites had different sediment compositions compared to the sediments at the reference sites (Table 5.7). Comparison between the low intensity and reference sites revealed a consistent R value, with significant differences evident in all years. The difference reflects the

variation of sediment composition at the reference site while the low intensity site recorded a fairly similar composition throughout the study period. Meanwhile, the R value showed significant difference between the high intensity and reference sites in all years. However, with respect to the overlapping of samples in the PCA, the value of dissimilarity between these sites decreased towards 2007.

Table 5.7: Summary of R-values derived from ANOSIM test (based on Euclidean distance) for composition of particle size in Area 222 from 2001 to 2004 and in 2007.

Technique	High intensity/Ref	Low intensity/Ref
2001	0.418**	0.347**
2002	0.610**	0.401**
2003	0.254**	0.405**
2004	0.215**	0.384**
2007	0.133*	0.364**

* Significant difference at $p < 0.05$. ** Significant different at $p < 0.01$

5.3.4 Effect of sediment composition on macrofaunal community structure

Distributions of plots for abundance and biomass data were overlaid on the sediment PCA ordination in order to explore the relationship between macrofaunal community and sediment composition (Figure 5.4). Macrofaunal abundance and biomass showed a pronounced relationship with gravel content, where this sediment fraction was generally associated with higher abundance ($r = 0.27$) and biomass ($r = 0.36$) of macrofauna. The coarse sand on the other hand, showed a lower association on the abundance ($r = -0.48$) and biomass ($r = -0.24$). Meanwhile, the association of sediment composition with species diversity indices was not obvious. Both the species richness and Margalef index (Dm) appeared to be high at sites dominated by gravel and fine sand ($r = 0.33$). A rather small number of samples show low association with silt/clay particles ($r = -0.11$). In contrast, a strong association is shown between Simpson index (Ds) with all particle sizes except silt/clay. Although there are some differences between the biotic compositions with the overall distribution of sediment particles, all data supports the suggestion that gravel is the most influential sediment fraction that structures the macrofaunal composition.

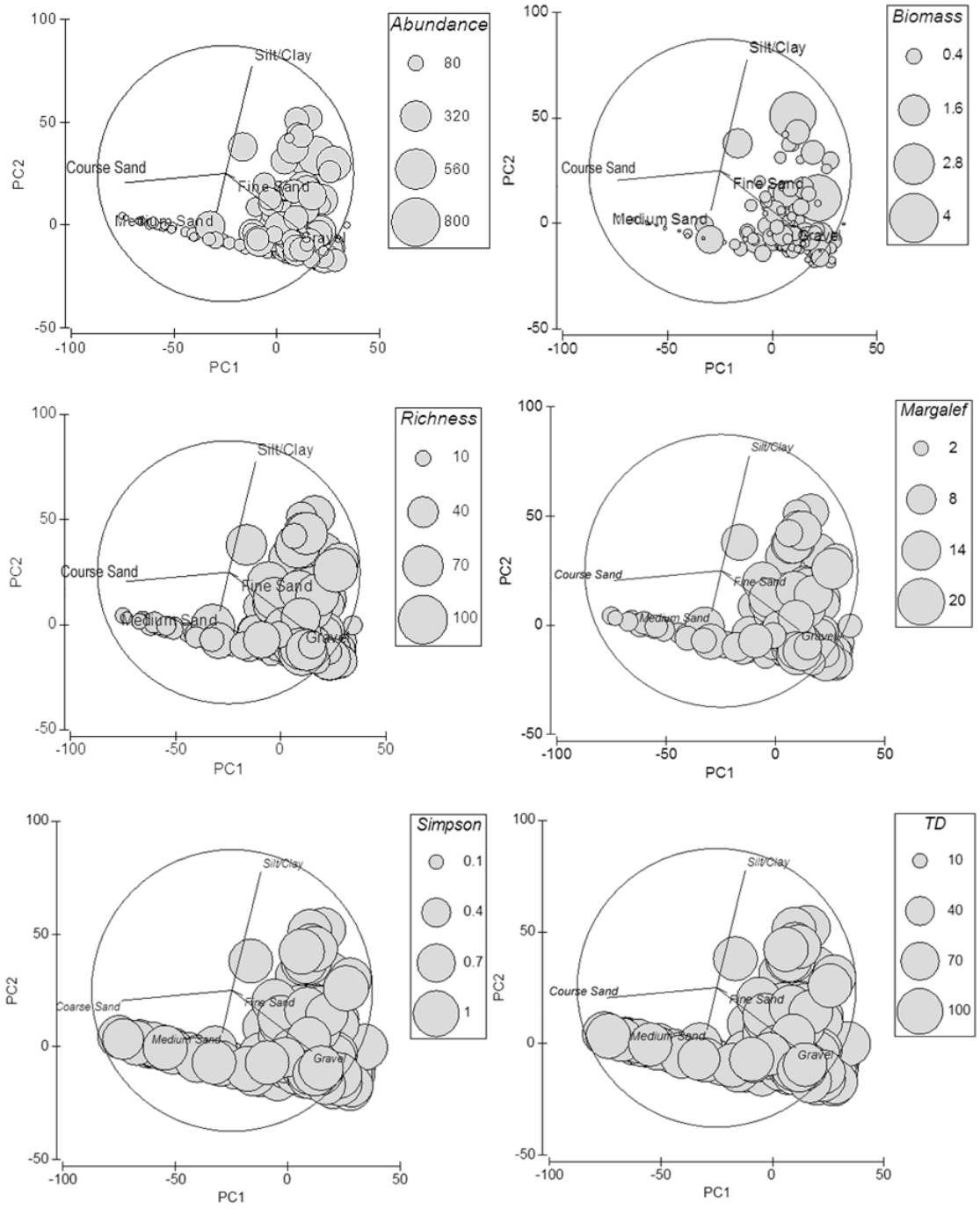

Figure 5.4. PCA ordination plot with superimposed bubble plots for Abundance, Biomass, Species richness, Margalef index, Simpson index and Taxonomic Distinctness (TD).

The plots of abundance of main characterising species were overlaid on the sediment PCA ordination in order to explore any evidence of sediment preference (Figure 5.5). All species showed high affiliation with gravel deposit with the highest affiliation showed by *Pomatoceros lamarcki* (r = 0.21). A small number of this species were also found in medium sand and fine sand dominated sediments. *Pisidia longicornis*

was also recorded in high number in gravel deposits (r = 0.07), but were also found in sediments with a high proportion of silt/clay. Apart from gravel, medium sand appears to have a high association on particular species namely *Lumbrineris gracilis* and *Lanice conchilega*, although both species were more strongly associated with gravel.

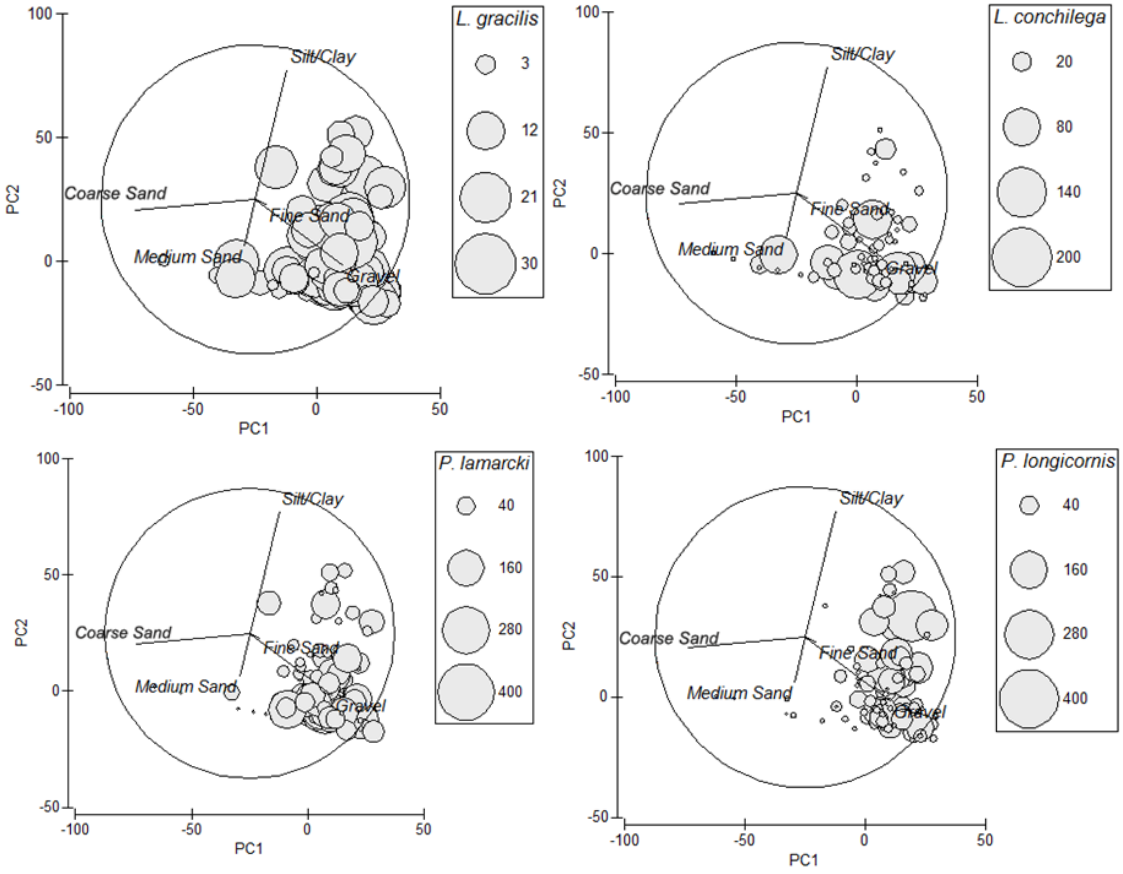

Figure 5.5. PCA ordination plot with superimposed bubble plots for the main characterising species found in gravel-dominated sediments.

The influence of gravel was also evident at sites dominated with finer sediments (i.e. the high intensity site in 2001 and 2002). Two main characteristic species (*Spisula* (juv.), r = 0.31; *B. crenatus*, r = 0.38) at this site also show a strong association with gravel (Figure 5.6). The relationship shows that the main characteristic species in gravel-dominated sediments tend to be found in only gravelly sediments. In contrast, dominant species in finer deposits were also found in gravel sediments.

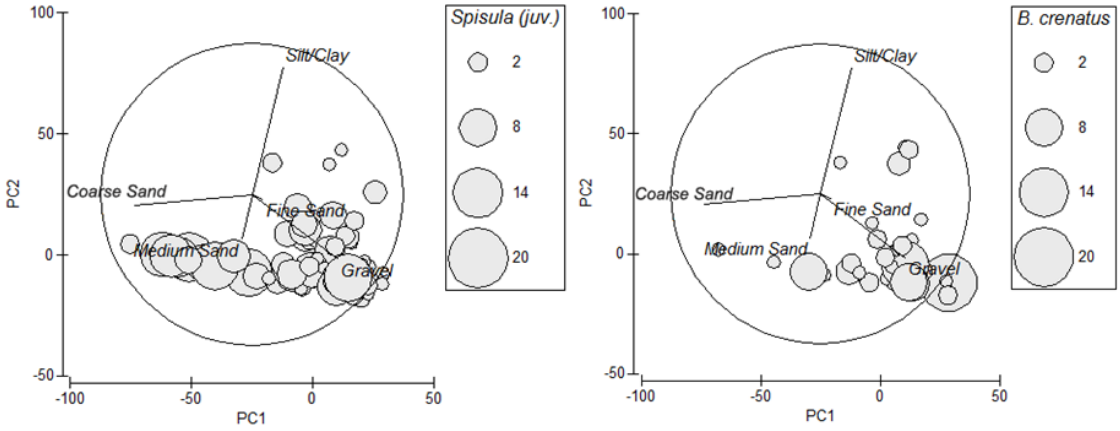

Figure 5.6. PCA ordination plot with superimposed bubble plots for main characterising species at fine deposit (i.e. the high dredging intensity site).

5.3.5 Effect of sediment composition on functional diversity

The influence of gravel deposit also can be seen on functional diversity indices, although the influence is not as strong as for biotic composition (Figure 5.7). The strongest influence of gravel was for Somatic Production (Ps) where high values of these indices were strongly associated with gravel deposits. Gravel also shows a strong influence on Infaunal Trophic Index (ITI), Rao's Quadratic Entropy (Rao's Q), and Functional Diversity (FD). However, high index values were also highly associated with medium sand and fine sand.

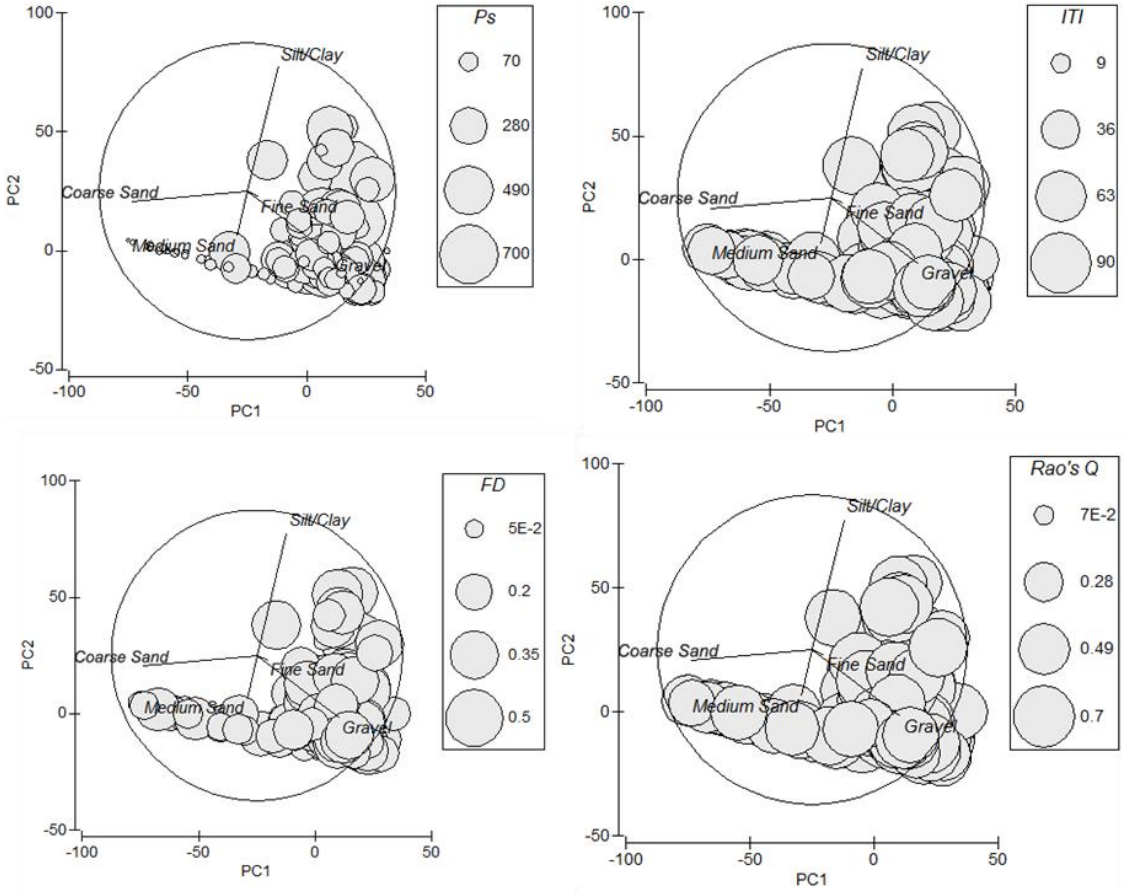

Figure 5.7. PCA ordination plot with superimposed bubble plots for Ps, BTA, ITI, Rao's Q and FD.

5.3.6 Influence of gravel on benthic community

Canonical analysis of principal coordinates (CAP) shows that the changes in macrofaunal assemblage structure across all sites over the study period was strongly related to the percentage of gravel deposit (canonical correlation of $\delta = 0.94$) (Figure 5.10). The community structure at both low dredging intensity and reference sites were constrained to the gravel dominated seabed, while the community at the high intensity site spread along the gravel gradient. The grouping of two samples from this site (year 2004 and 2007) shows that, with increasing percentage of gravel, the macrofaunal community in those years became more similar to communities under reference conditions.

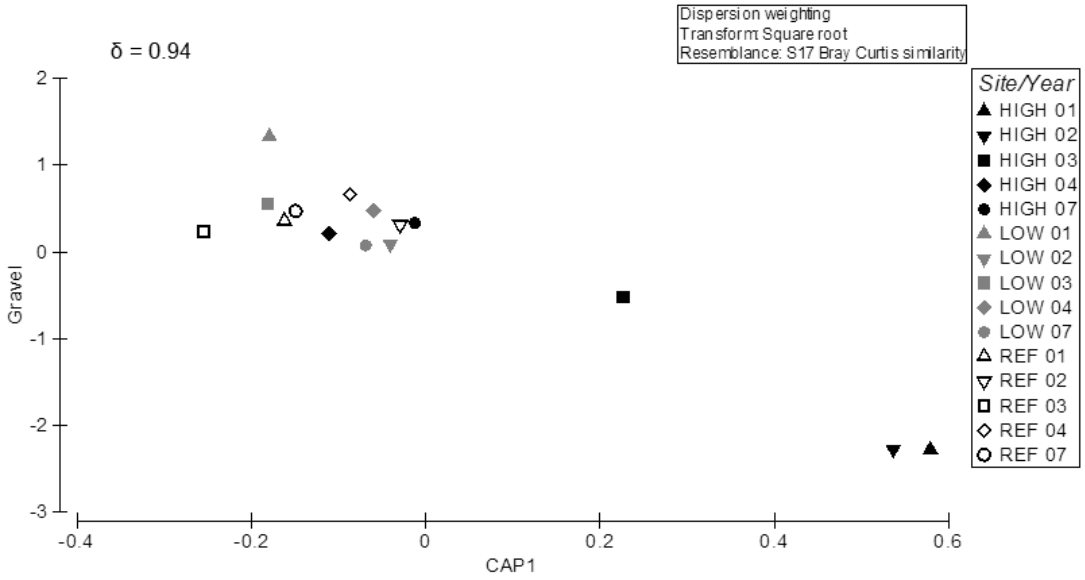

Figure 5.10. Canonical analysis of principal coordinates (CAP) relating abundance from sites in Area 222 to the percentage of gravel deposit. Each point represent average abundance at all sites in specific years (3 sites x 5 years = 15 points). The analysis was based on Bray Curtis dissimilarities calculated from square-root transformed abundances.

5.4 Discussion

The impact of aggregate dredging on the seabed environment is site specific and depends on several factors including dredging methods, seabed topography, current strength and sediment type and mobility (Desprez, 2000). The physical changes caused by this activity relate to removal of the sediments, seabed topography alteration, changes in sediment composition and re-deposition of sediment particles (De Groot, 1996; Newell et al., 1998). The present study shows that the impact of dredging on sediment composition was apparent at the site with higher dredging intensity where this site contained finer sediments with proportionally more sand than gravel. Such change was less apparent at the site with lower dredging intensity. During the initial extraction process, significant amounts of sediments are removed regardless of their sizes. Therefore, the change of sediment composition is not principally due to the removal, but the change is ultimately the product of the later processes. Physical marks (e.g. pits and furrows) imposed by the dredger change the dynamics of the bottom current; and depending on local environmental conditions, the pits and furrows may be filled with different deposits from surrounding areas resulting in a change of sediment composition (Kenny and Rees, 1996; Desprez, 2000). Additionally, application of screening and the inevitable overspill also returns

the finer deposits, especially sands to the seabed, which can then lead to a change in sediment composition (Newell et al., 1998; Boyd et al., 2004).

In terms of sediment characteristics, the site with higher dredging intensity showed different values of sorting, skewness and kurtosis compared to the other sites. Although all sites were generally poorly sorted, sediments at the high intensity site were better sorted. This finding is in accord to study by Trimmer et al. (2005) who observed an increase in sediment sorting within an area of intensive trawl fishing. The better sorting at this site as compared to the low intensity and reference sites is explained by the factor of grain size. According to Tucker (2001), sand size sediments are more easily transported by water and thus are more likely to create better sorted sediments. In the present study, larger sediments at the low intensity and reference sites, with the dominance of gravel, contributed strongly to the poor sediment sorting level. According to Ahmad (1990), the most sorted sediments are generally medium sands and the sediments at either size of this category are more poorly sorted. In addition to water currents, depositional process also contribute to the sediment composition, and the effects of deposition can be seen on skewness (Mohd-Lokman and Pethick, 2001; Tucker, 2001). All sites were positively skewed indicating a mode of coarse particles with a substantial fraction of finer particles. The greater proportion of finer particles may be explained by local hydrodynamic conditions where these particles were not removed by the current but rather trapped between larger particles or trapped in the dredge furrows (Cronan, 1972; Tucker, 2001). In this study, gravel appeared to be very influential as the dominance of this particle size substantially increases the kurtosis value.

The sediments at the high intensity site also showed a higher degree of variability compared to other sites. The high variability of sediment composition at dredged sites was also reported in studies by Kenny and Rees (1994) and Sárda et al. (2000). According to Boyd et al. (2005), this could be the effect of patchy sediment distribution created by uneven impact of dredger's draghead on the seabed. Without further photographic and bathymetric investigation, it is impossible to explain the compositional change in relation to the seabed topography. Nevertheless, it is hypothesised that this could be due to the eradication of sand waves at the site which had developed in previous years (Boyd et al., 2004). The natural variability and the patchiness of sediments before dredging (Boyd et al., 2004) may not be erased by

the activity and still contribute to post-dredging variation. While the increase in the amount of gravel at the low intensity site took place earlier, an increase at the high intensity site was observed in 2003 where a significant amount of gravel and a reduction of coarse sand were recorded. Sediment composition at the low intensity site also showed a different composition to the reference site. Although the general features of the sediments were different, some similarity was recorded at least in terms of gravel fraction throughout the study period. Since this study was first carried out five years after dredging ceased, the definite recovery of gravel deposit at the low intensity site is not known. However, the findings from this study show how excessive and frequent disturbance may have led to a more severe physical change. With the less intense dredging, the transport of sands away from this site might balance the deposition of sand particles from overspill or screening (Boyd et al., 2004).

The additional dataset from 2007 included in the present study is consistent with the trend of an increasing gravel fraction at the high intensity site as shown by Boyd et al. (2004) and Cooper et al. (2005) for previous years. This finding improves confidence in the suspected natural physical recovery ongoing at the high intensity site. Although the PCA shows that sediment samples at the dredged sites are still different from the Reference site, the data suggest that the increase of gravel fraction is becoming more comparable to the Reference site. Based on the sediments composition at all sites, gravel and coarse sand were clearly the main particles that showed a substantial variation over the period of the study. Therefore, this provides the insight that these particle fractions may, at least in part, be responsible for the observed differences in macrofaunal communities between sites.

Given that the present study only assessed sediment particles without additional information such as topography and hydrodynamic data, the changes in seabed habitat following dredging need to be interpreted with care. The first aspect that might influence the similarity and difference between samples was the patchiness of the seabed following dredging. Although the high intensity site recorded a more apparent patchiness compared to the other sites (Boyd et al., 2004; Cooper et al., 2005), the way samples were collected (randomly) could cause inconsistency (i.e. whether inside or outside the dredge furrows).

A core theme in benthic ecology is to characterise the relationship between animal and sediments (Gray, 1974; Constable, 1999). Many studies have reported the positive correlation between macrofaunal abundance and sediment stability (Death and Winterbourn, 1995; Death, 1996; Townsend et al. 1997). Stable substrata are suitable habitats for many invertebrate species due to the stable platform provided, and also because minimal bedload transport allows a high level of food resource for the fauna to be maintained (Walton et al., 1977; Rosenberg and Wiens, 1978; Wagener and LaPerriere, 1985; Death, 2000; Jowett, 2003). However, finer deposits could also be beneficial as they provide a more suitable habitat for deposit feeders than the coarser deposits which favour suspension feeders (Rhoads and Young, 1970; Gray, 1974).

Due to the nature of the data collected, the present study has emphasised the importance of gravel in promoting the recovery of macrofauna. The importance of gravel in providing a stable habitat with a rich food source is shown for macrofaunal structure and functional diversity. The present study therefore supports and extends the work of Boyd et al. (2004) and Cooper et al. (2005). Almost all indices and characteristic species show higher values or biomass corresponding exclusively to the gravel-dominated sites. Some indices were variable where higher values were also recorded in association with other sediment fractions. While gravel was the most influential factor, Simpson index, Taxonomic Distinctness, Infaunal Trophic Index also showed higher values allied to coarse sand and medium sand. This is explained by the high values of these indices recorded at the high intensity site (see Chapter 3 and 4). Out of four main characteristic species, only *Lumbrineris gracilis* was not confined exclusivity to gravel deposits. This species is naturally common in both gravel and sand-dominated sediments (Cooper et al., 2011). The other main characteristic species (*Pomatoceros lamarcki*, *Lanice conchilega* and *Pisidia longicornis*) showed a high association with gravel deposit, but it is difficult to determine whether these species are really gravel specialists. Clearly, this can be investigated in the future by examining more datasets that comprise the sites with various sediment characteristics.

As reported in the study by Cooper et al. (2011), the loss of gravel may lead to the structural and functional changes of macrofaunal communities in many dredging sites around the UK. This is supported in the present study since many of the

characteristic species were strongly associated with the gravel deposits. However, the main characteristic species from finer sediments also recorded a strong association with gravel. The importance of gravel in both gravel-dominated and sand-dominated habitats could lead to the severe impact on the macrofaunal community when gravel is removed through physical disturbance.

5.5 Conclusion

Dredging intensity was the main factor that determined the level of disturbance in Area 222, and this factor also influenced the time taken for the site to recover. The site with lower dredging intensity recorded a faster physical recovery in the sense that the similarity of gravel composition with the reference sites took place earlier than at the higher intensity site. Due to the lack of data on other physical parameters, the relationship between fauna and environmental variables was focussed only on sediment grain size, in particular, gravel, which showed great variation over time. Although study of the sediment characteristics helps to focus on the relationship between macrofauna and environmental factors it is confined to a narrow range of variables and this is also something to be wary of in the sense that macrofaunal responses to other physical parameters may determine their distribution (Gray, 1974). As discussed above, factors such as the strength of the currents and processes at sediment-water interface also affect macrofaunal community distribution. Clearly, a causal mechanistic study which involved all of the realistic complexities of various factors for the seabed environment is needed to provide a better insight to the animal-sediment relationships. The measurements used in the present study were at least able to provide an initial predictive outline, with the realisation that many intrinsic factors are still being ignored.

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Chapter 6: Functional response of benthic macrofauna to dredging impacts

6.1 Introduction

The interaction between organisms and their environment is an important factor that structures ecosystem function. Understanding the interactions which can take place through feeding behaviours, environmental preference and life habits is necessary in furthering our knowledge of the consequence of anthropogenic and natural changes on the functioning in marine ecosystems. Information from this interaction will also be useful in determining the environmental status of an area after disturbances, and may also be valuably employed to assess the impact that any future changes may impose.

Prior to investigating the interaction between fauna and their environment, functional diversity of marine benthic communities has been assessed based on taxonomic composition. This indirect measure requires that the change in taxonomic composition implicitly change the ecological characteristics exhibited by different taxa. This approach is however unable to discriminate which functions or traits are responsible for the environmental change (Bremner et al., 2003). Therefore, a more targeted approach that directly measures the species' traits should be used in the study of functional diversity. Although species traits analysis is generally considered to be a better way to assess ecosystem function than species or taxonomic composition (Tilman et al., 1997; Hulot et al., 2000; Díaz and Cabido, 2001; McGill et al., 2006; Naeem, 2009), its measurement can be more complicated and time consuming. Many ecologists have proposed methods to quantify functional diversity, and these are generally based on two main approaches, with both approaches classifying the species into traits such as environmental preference, behavioural and morphological characteristics (Bremner et al., 2003; Petchey and Gaston, 2006). The first approach is relatively straight forward and classifies the species into any one function, which are then subjected to analysis using conventional mathematical techniques such as diversity indices (Stevens et al., 2003; Botta-Dukat, 2005; Petchey and Gaston, 2006). The second approach classifies the species based on a combination of multiple traits and appoints a value based on their affinity to the traits (e.g. Bremner et al., 2003; Charvet et al., 2000; Lepš et al., 2006). This approach is relatively more complicated than the previous one since one species can be

classified into multiple traits, and the classification also demands a judgement as to how the species is valued for given traits.

The interaction between fauna and environment in the present study was based on feeding mechanisms and motility, where taxa were combined into specific groups to investigate the distribution and composition of the trophic groups across different sites that experienced different environmental stresses. The literature information of the use of both traits is scarce (e.g. Barrio Froján, 2005). However, there are a large number of studies that have utilised feeding behaviours to investigate pollution effects (Gaston et al., 1998; Maurer et al., 1999; Mistri et al., 2000), habitat modification through bottom trawling (Garrison and Link, 2000) and dredging (Cooper et al., 2008; Barrio Froján et al., 2011). The technique used in the present study was based on the first approach (see above) where species were assigned to the particular trait that best described the species in question. The selection of this approach was to simplify the interpretation, and reduce any possible discrepancies as a result of multiple traits being assigned to single species.

The present study aimed to determine the relative proportion of different functional groups in Area 222 and investigate any change in structure following the impact of marine aggregate dredging. Recovery of the functional groups' proportion was determined at both the low and high dredging intensity sites. Based on the traditional indices data (Chapter 3), it is hypothesised that the low intensity site would functionally recover (or progress towards recovery) earlier than the high intensity site. This was achieved by comparing the abundance and species diversity that represented each functional group in dredged sites with the undisturbed (reference) site. In addition, this study also investigated the effect of the functional groups in shaping the community structure in the area. Recognising the influence of sediment particle size on benthic community structure and functioning, analysis was also carried out to determine which grain size had the strongest link to particular functional groups. Through understanding the benthic community at the functional level (rather than the species level) this study can usefully contribute to a better understanding of ecosystem function in a simple way without neglecting its most important information about the interaction with the environment. It is acknowledged that by simplifying the assessment, there are several important traits that may be dismissed. However, considering the use of multiple traits could increase the inaccuracy of assigning

species to specific traits, this chapter offers an alternative way of measuring recovery of ecosystem function based on the traits that are believed to be the most important. In addition, the approach used in this study looks in more detail into the effect of dredging on the functionality of the community. By doing this, this study will provide useful information and act as a reference for managing the ecosystem on a functional level.

6.2. Methods

6.2.1 Functional groups classification

The benthic faunal species were classified according to their feeding mechanisms and motility following Fauchald and Jumars (1979), and where no information was available, the classification used in the Infaunal Trophic Index together with Biological Traits Analysis (see previous chapter) were referred to. In the case of no traits information being available, the functional groups were assigned by referring to the most similar species in the same genus or family based on expert judgement. The functional groups were motile carnivores, motile omnivores, motile surface deposit feeders, motile sub-surface deposit feeders, motile filter feeders, sessile filter feeders, sessile deposit feeders and sessile carnivores (see Table 6.1 for a full description of every function).

As the macrofauna community was classified into functional groups, the recovery (functional recovery) was defined as the range functional groups in dredged sites becoming proportionally similar to the reference site. Based on the analysis presented in previous chapters, it seems unlikely that the disturbed community would ever become exactly similar to the community before dredging. Therefore, this chapter treats the return of the main functional group as the indication of functional recovery.

Table 6.1. Description of functional groups used to classify the benthic species based on their motility and feeding mechanisms. The classification of Polychaete species was based on Fauchald and Jumars (1979), and other species were classified followed the methods in the Infaunal Trophic Index and Biological Traits Analysis.

Functional groups	Description	Examples
Motile carnivores (MC)	Species are characterised by displaying prominent jaws. They feed by preying on other fauna or by scavenging, which results in the loss of benthic fauna from other groups.	*Asterias rubens* (Echinodermata) and *Atelecyclus rotundatus* (Crustacea)
Motile omnivores (MO)	Species with prominent jaws as in MC. Feed on other fauna and sometimes, depending on the prey availability and environmental condition, they may become herbivore, detritus and deposit feeders.	*Cancerilla tubulata* (Crustacea), *Lumbrineris gracilis* (Polychaeta)
Motile surface deposit feeders (MSDF)	Feed by capturing food particles using their tentacles. The foods are normally captured from the sediment surface, but sometimes from the water column depending on the speed of the near-bed flow.	*Amphipholis squamata* (Echinodermata), *Aonides oxycephala* (Polychaeta)
Motile sub-surface deposit feeders (MSSDF)	As the MSDF, they feed on deposit particles, but the foods are obtained through the act of sediment burrowing. These fauna obtain food by either directly ingesting sediment particles or by selecting a suitable range of particle sizes	*Anthura gracilis* (Crustaea), *Echinocardium cordatum* (Echinodermata)
Motile filter feeders (MFF)	Mobile species which actively feed on microscopic organisms which are free-floating in the water by drawing the water through their body.	*Ensis americanus* (Mollusca), *Rissoides desmaresti* (Crustacea)
Sessile filter feeders (SFF)	This group is comprised of mainly tube-dwelling organisms. The feeding strategies are through the act of extending tentacles to collect floating food particles or through pumping water over sticky mucus net for subsequent ingestion.	*Pomatoceros lamarcki*, (Polychaeta), *Lanice conchilega* (Polychaeta)
Sessile surface deposit feeders (SSDF)	Tube-dwelling organisms that are characterised by long tentacles. The tentacles are extended on the sediment surface to collect food particles.	*Thelepus cincinnatus* (Polychaeta),*Pseudopotamilla reniformis* (Polychaeta)
Sessile carnivore (SC)	This group is characterised by predatory species that attach on the surface. Their feeding strategies normally involve poisoning or entangling prey.	Mainly Cnidaria such as *Clytia hemisphaerica* and *Sertularia cupressina*

6.3 Results

6.3.1 Univariate measure

The proportion of functional groups over time was dominated by sessile filter feeders at the high dredging intensity site where the dominance of this group was evident in 2007 (Figure 6.1). The abundance of sessile filter feeders was significantly different between the high intensity and reference sites in the early years of study period ($p < 0.05$) (except in 2001), but no difference was recorded in 2007 ($p > 0.05$). The low intensity site also recorded a fairly similar proportion with the reference site throughout the study period.

There was a similar trend in distribution of species richness within the functional groups at all sites throughout the study period (Figure 6.2). Similar to abundance, sessile filter feeder generally contributed to the highest proportion of species richness. At the high intensity site, sessile filter feeders were recorded in the highest proportion in 2001 with 34%, followed by motile carnivores with 25%. However, motile carnivores became the top contributor in subsequent years, but in 2007 sessile filter feeders once again dominated the proportion in terms of number of species. This proportional trend was comparable to the reference site which recorded sessile filter feeders as the richest species throughout the period followed by motile carnivores. The low intensity site recorded a higher similarity with the reference site for the proportion of number of species. The highest species richness in this site was recorded for sessile filter feeders throughout the study period, with the exception of 2003 where motile carnivores comprised the highest number of species (28%) compared to sessile filter feeders (23%).

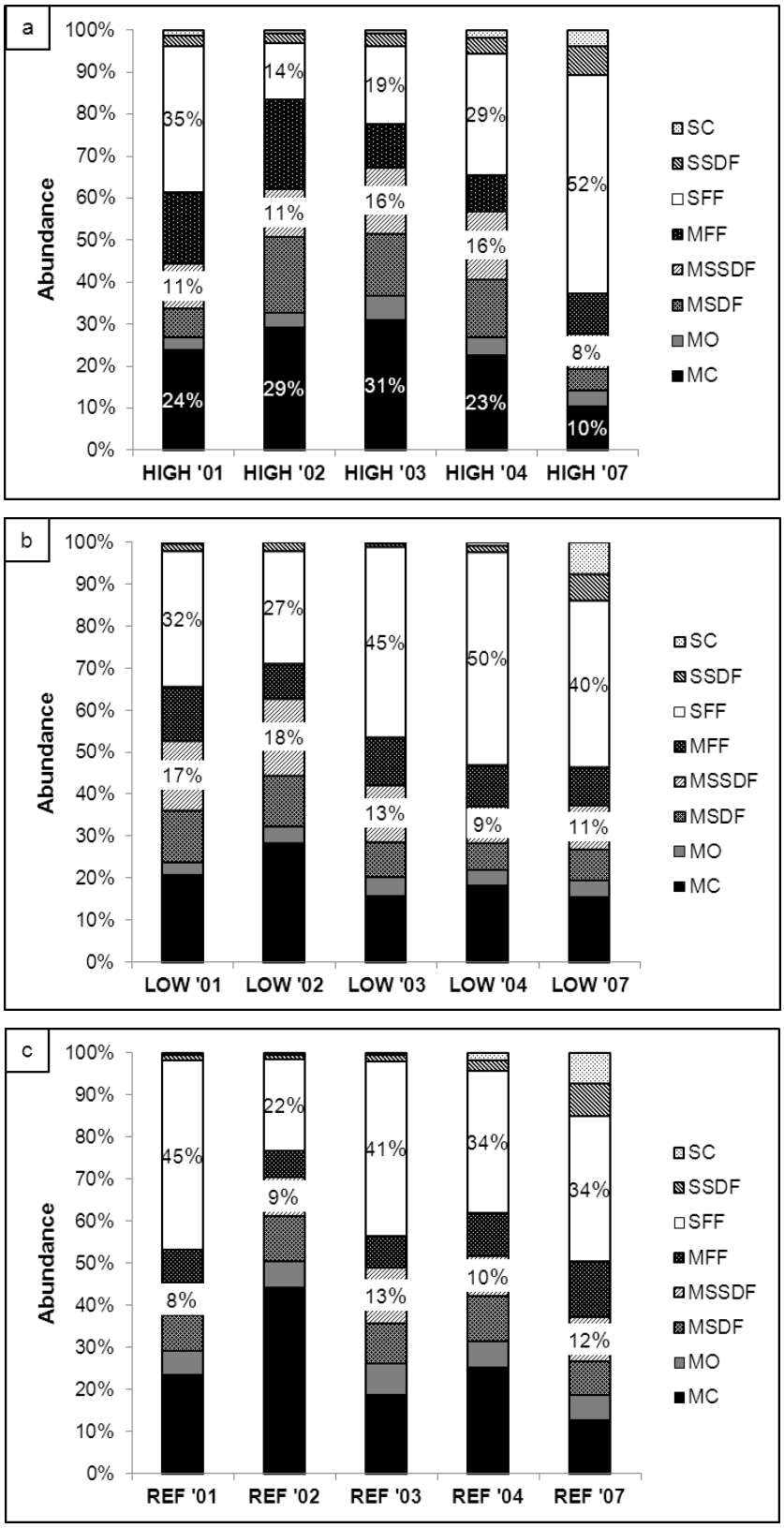

Figure 6.1. The proportion of number of species that represents each functional groups at a) high dredging intensity, b) low dredging intensity c) reference sites for the year 2001 to 2004 and 2007.

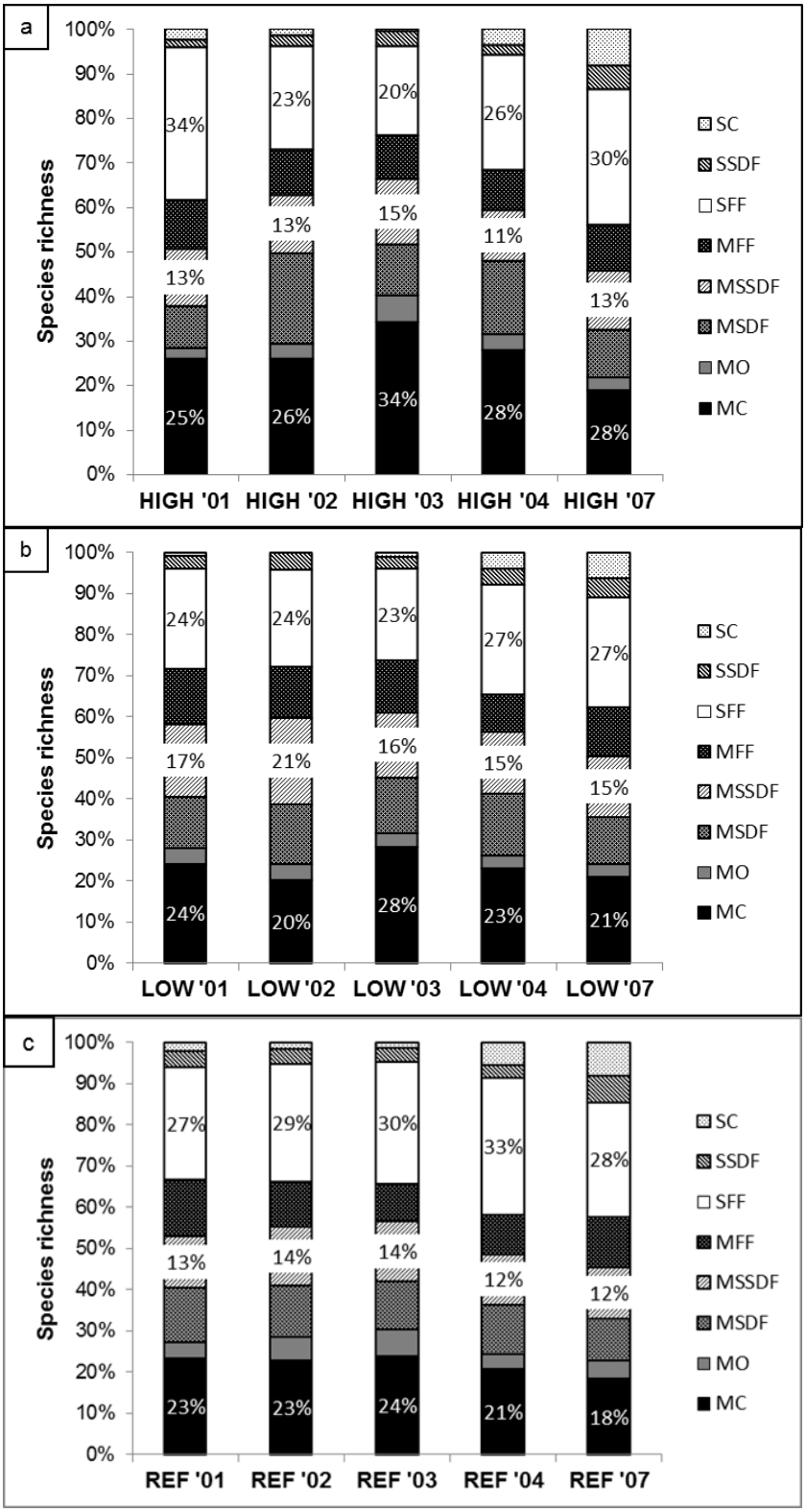

Figure 6.2. The proportion of number of species that represents each functional groups at a) high dredging intensity, b) low dredging intensity c) reference sites for the year 2001 to 2004 and 2007.

The mean number of sessile suspension feeders in 2007 at the high intensity, low intensity and reference sites was 58.3, 101.4 and 44.1 respectively. The predominance of the polychaete *Pomatoceros lamarckii* with a total proportion of 19.7% is believed to result in the difference of functional group proportions especially between the high and low intensity sites (Table 6.2). This species recorded a substantial increase of abundance from 2001 to 2007 at the high intensity site to become the most dominant group, as recorded at the low intensity site. The reference site was dominated by *Pisidia longicornis* which is a motile carnivore, although the contribution of sessile filter feeder to the proportion of the group at this site is still high due to the presence of *P. lamarcki* (the second most abundant species)and *Lanice conchilega* (the third most abundant species).

Table 6.2. List of the 5 most dominant taxa at the high and low dredging intensity sites and the reference site. The list is based on the total abundance of the taxa recorded from 2001 to 2004 and in 2007.

HIGH	**2001**	**2002**	**2003**	**2004**	**2007**
Pomatoceros lamarcki	1	4	15	81	379
Spisula (juv.)	39	66	3	12	27
Spisula solida	41	66	3	12	2
Serpulidae	-	3	5	35	73
NEMERTEA	11	28	15	25	23

LOW	**2001**	**2002**	**2003**	**2004**	**2007**
Pomatoceros lamarcki	43	349	803	1820	609
Pisidia longicornis	89	430	152	598	82
Serpulidae	20	87	182	468	76
Ophiura (juv.)	36	33	129	334	86
Lumbrineris gracilis	36	75	105	168	89

REF	**2001**	**2002**	**2003**	**2004**	**2007**
Pisidia longicornis	368	919	116	290	21
Pomatoceros lamarcki	336	255	388	298	82
Lanice conchilega	545	15	6	4	85
Serpulidae	137	78	141	163	8
Lumbrineris gracilis	93	126	109	113	85

6.3.2 Multivariate measure

The non-metric Multidimensional Scaling (MDS) shows that samples from the low intensity and reference sites are clustered together which indicates a high degree of similarity for both abundance and species richness of functional groups (Figure 6.3). Meanwhile, samples from the high intensity site are widely dispersed to the right-hand side of the plot. The MDS also shows overlapping of the samples (especially in

2004 and 2007) from the high intensity site with the reference sites which indicates that the high intensity site became more similar to the reference sites approximately 8 years after dredging ceased. The similarity pattern of the samples is confirmed by ANOSIM R values (Table 6.2) that shows as the overlapping of the MDS plot suggested, the difference between high intensity and reference sites was relatively smaller in 2004 and 2007 compared to the earlier study period.

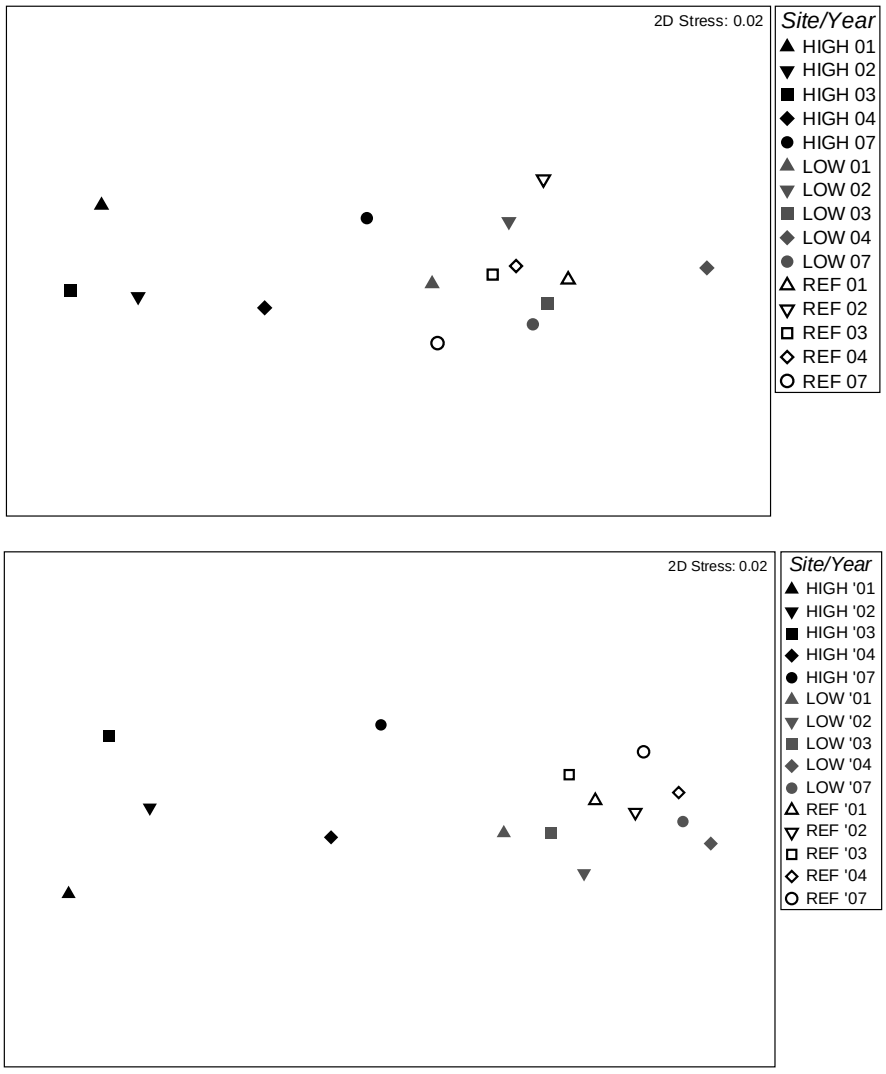

Figure 6.3. An MDS plot of Bray Curtis Similarity of the distribution of functional groups based on abundance (top) and species richness (bottom) at the high intensity, low intensity and reference sites from 2001 to 2007. The ordination is based on Bray-Curtis similarity values.

Table 6.2. Summary of R values derived from ANOSIM test of the abundance of macrofauna in different functional groups.

Measurement	High/Ref	Low/Ref
Abundance		
2001	0.856*	0.529*
2002	0.950*	0.124
2003	0.878*	0.007
2004	0.367*	0.557*
2007	0.323*	0.396*
Richness		
2001	0.771*	0.290*
2002	0.890*	0.499*
2003	0.662*	0.081
2004	0.530*	0.106
2007	0.456*	0.004

* significant different at $p<0.01$

The influence of sessile filter feeders that contributes to the similarity of the samples is shown by cluster analysis (Figure 6.4a). From 2001 to 2004, this group recorded only 23% resemblance between the samples from the high intensity and reference sites, but this rose to an 88% resemblance in 2007. The difference was less apparent between the low intensity and reference sites with the resemblance ranging from 71% to 99% between 2001 and 2007. There was no influence to the similarity of the samples in 2007 from the second most abundant group, motile carnivore (Figure 6.4b). The resemblance between the high intensity and reference sites was 39% for the whole period of study.

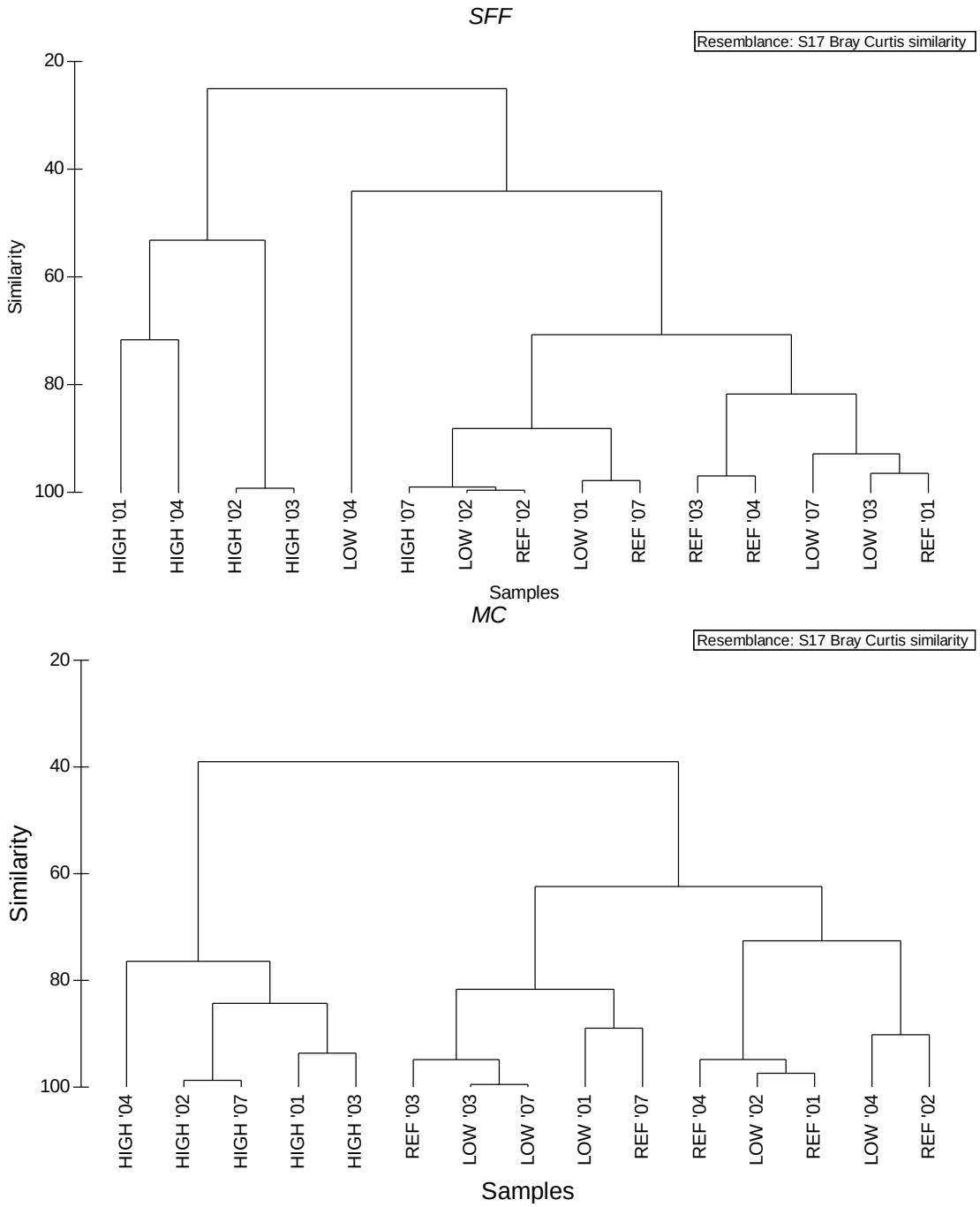

Figure 6.4. Ordination dendogram of the similarity between the sites based on the composition of the most dominant functional groups of sessile filter feeders (SFF) and motile carnivores (MC). The similarities between the sites were clustered using Bray-Curtis values.

The single functional variable that best determined the ordination of the high intensity site in relation to the faunal structure was MO (ρ_w =0.361) and followed by MSDF and SFF with ρ_w =0.351 and 0.344 respectively (Table 6.4). The Spearman rank correlation value increased as the number of variables increased. MO was influential

on the ordination at the high intensity site: this functional group was in almost all combination variables. The overall optimum value was recorded by the 5-best combination variables of MO, MSDF, SFF, SSDF, SC with a correlation value of ρ_w =0.532. The functional groups that best determined the ordination remained the same from 2001-2004, but changed with data from 2007. At this time, SFF appeared to be the best single variable to determine the ordination of the samples with ρ_w =0.360 (Table 6.5). Similar to data for the whole period, the correlation values also increased when variables were added. The combination with the lowest correlation value contained the sessile filter feeders (SFF, MO, SSDF, ρ_w =0.360).

Table 6.4. Combination of variables giving the highest rank correlations between functional and structural similarity matrices at the high dredging intensity site throughout the study period. The highest correlation value is given in bold font.

Number of variables	Best variable combination	Spearman rank correlation (ρ_w)
1	MO	0.361
1	MSDF	0.351
1	SFF	0.344
2	MSDF, SFF	0.462
2	MSDF, SSDF	0.404
2	MO, MSDF	0.403
3	MO, MSDF, SFF	0.505
3	MSDF, SFF, SSDF	0.494
3	MSDF, SFF, SC	0.471
4	MO, MSDF, SFF, SSDF	0.524
4	MO, MSDF, SFF, SC	0.512
4	MSDF, SFF, SSDF, SC	0.501
5	**MO, MSDF, SFF, SSDF, SC**	**0.532**
5	MO, MSDF, MSSDF, SFF, SSDF	0.495
5	MO, MSDF, MSSDF, SFF, SC	0.487
6	MO, MSDF, MSSDF, SFF, SSDF, SC	0.500
6	MO, MSDF, MFF, SFF, SSDF, SC	0.491
6	MO, MSDF, MSSDF, MFF, SFF, SSDF	0.475

Table 6.5. Combination of variables giving the highest rank correlations between functional and structural similarity matrices at the high dredging intensity site in 2007. The highest correlation value is given in bold font.

Number of variables	Best variable combination	Spearman rank correlation (ρ_w)
1	SFF	0.360
1	MO	0.296
1	SSDF	0.248
2	SFF, MO	0.473
2	MO, MSDF	0.465
2	SFF, SSDF	0.454
3	**SFF, MO, SSDF**	**0.545**
3	SFF, MO, SC	0.483
3	SFF, MO, MSDF	0.471
4	SFF, MO, SSDF, SC	0.537
4	SFF, MO, MSDF, SSDF	0.529
4	SFF, MO, MSSDF, SSDF	0.481
5	SFF, MO, MSDF, SSDF, SC	0.511
5	SFF, MO, MSDF, MSSDF, SSDF	0.496
5	SFF, MO, MSSDF, SSDF, SC	0.484
6	SFF, MO, MSDF, MSSDF, SSDF, SC	0.484
6	SFF, MO, MSDF, SSDF, SC, MC	0.463
6	SFF, MO, MSSDF, SSDF, SC, MC	0.454

6.3.3 Sediment characteristics and functional groups

The correlation between the environmental variables and macrofaunal functional patterns at the high dredging intensity site is summarised (Table 6.6). The single environmental variable that had the highest influence in grouping the sites to be consistent with the faunal patterns was the coarse sand (ρ_w =0.321), followed by gravel (ρ_w =0.246) which was lower by a factor of 1.30. The best 2-variable combination also involved the coarse sand with the addition of silt/clay (ρ_w =0.338), and coarse sand with medium sand (ρ_w =0.326). As the correlation value of coarse sand as a single variable is high, it is unsurprising to see that this variable appears in every combination. The high influence of the coarse sand is evidenced by the decreasing correlation values with the presence of other variables. However, when the analysis was constrained to only 2007 data, gravel was the best single environmental variable in clustering the samples to be consistent with the ordination of the faunal assemblage (ρ_w =0.326) (Table 6.7). The strong influence of gravel was demonstrated by considering that the second best single variable (sily/clay) was lower by a factor of 3.4. Combination of gravel and fine sand emerged as the best combination variables with a value of ρ_w =0.354.

Table 6.6. Combination of variables giving the highest rank correlations between functional and environmental similarity matrices at the high dredging intensity site throughout the study period. The highest correlation value is given in bold font.

Number of variables	Best variable combination	Spearman rank correlation (ρ_w)
1	coarse sand	0.321
1	gravel	0.246
2	**coarse sand, silt/clay**	**0.338**
2	coarse sand, medium sand	0.326
3	gravel, coarse sand, silt/clay	0.333
3	coarse sand, medium sand, silt/clay	0.325
4	gravel, coarse sand, medium sand, silt/clay	0.330
4	gravel, coarse sand, medium sand, fine sand	0.313

Table 6.17. Combination of variables giving the highest rank correlations between functional and environmental similarity matrices at the high dredging intensity site in 2007. The highest correlation value is given in bold font.

Number of variables	Best variable combination	Spearman rank correlation (ρ_w)
1	gravel	0.329
1	silt/clay	0.096
2	**gravel, fine sand**	**0.354**
2	coarse sand, fine sand	0.303
3	gravel, coarse sand, fine sand	0.327
3	coarse sand, medium sand, fine sand	0.284
4	gravel, coarse sand, medium sand, fine sand	0.271
4	gravel, coarse sand, fine sand, silt/clay	0.313

The association of sessile filter feeders (the most dominant group) and particular sediment particle size differed over time. In 2001, this group was most abundant (>50%) in fine and medium sand areas (Figure 6.5a), and had almost no association with gravelly sediment. However, 6 years after that, this group recorded around 40% association with gravel (Figure 6.5b). The trend of association of sessile filter feeders with gravel at the high intensity site in 2007 was in accord with the trend at the reference site (Figure 6.6).

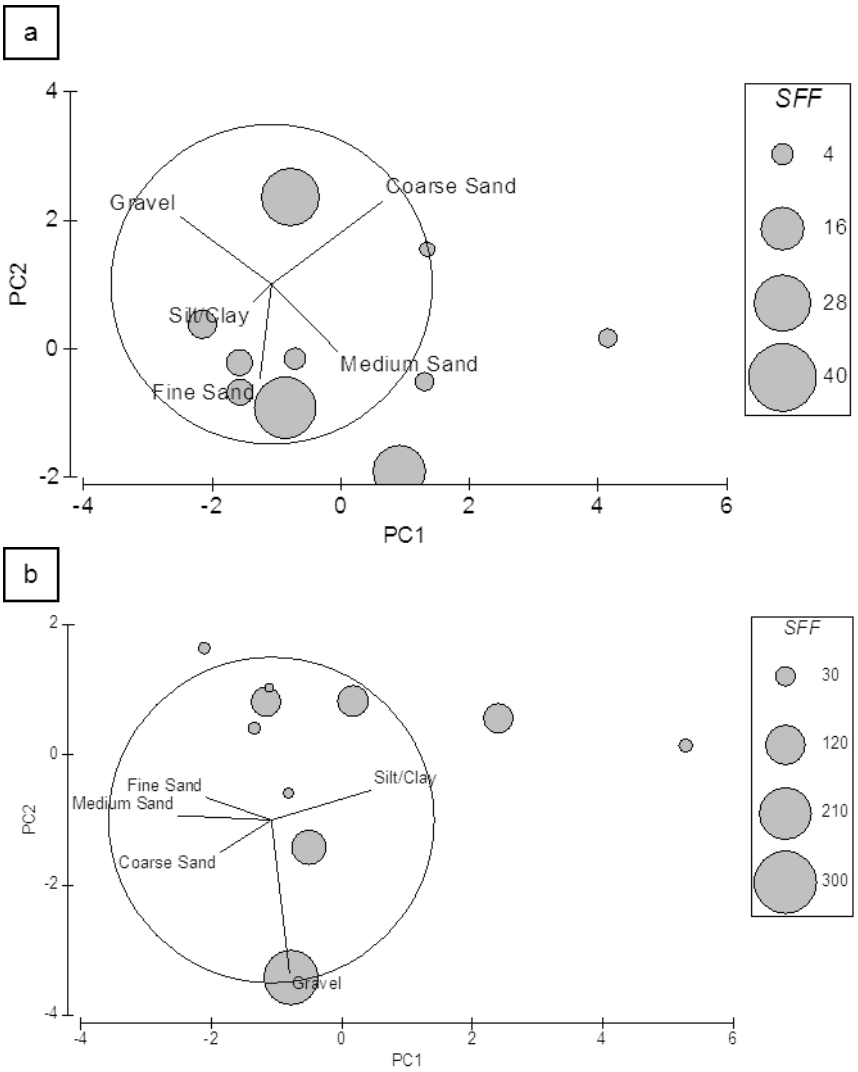

Figure 6.5. Principle component analysis (PCA) plots based on sediment particle size data with superimposed bubble plots for sessile filter feeders at the high dredging intensity site in a) 2001 and b) 2007.

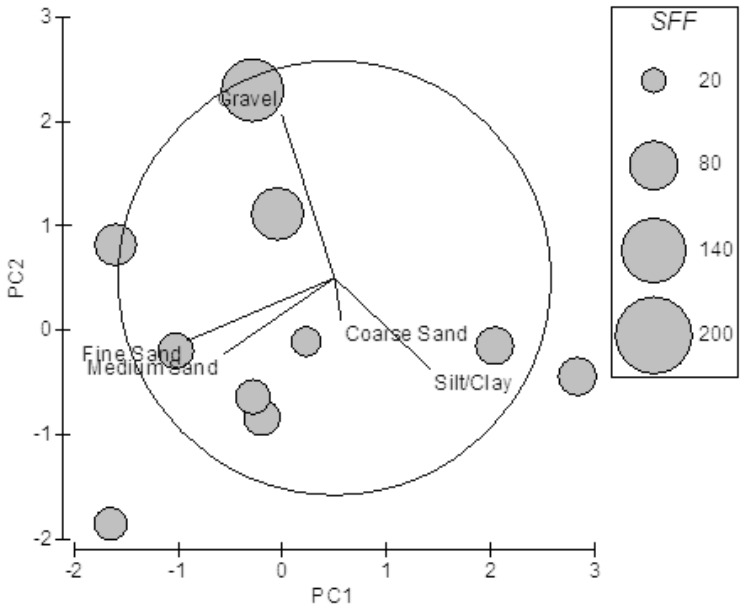

Figure 6.6. Principle component analysis (PCA) plots based on sediment particle size data with superimposed bubble plots for sessile filter feeders at the reference site in 2007.

The association with sediment particle size was not apparent in the second most dominant group, motile carnivores. This group was most commonly distributed within sandy sediment and almost no association with gravel was recorded in 2001 (Figure 6.7a). There was a low degree of association recorded in 2007 (Figure 6.7b).

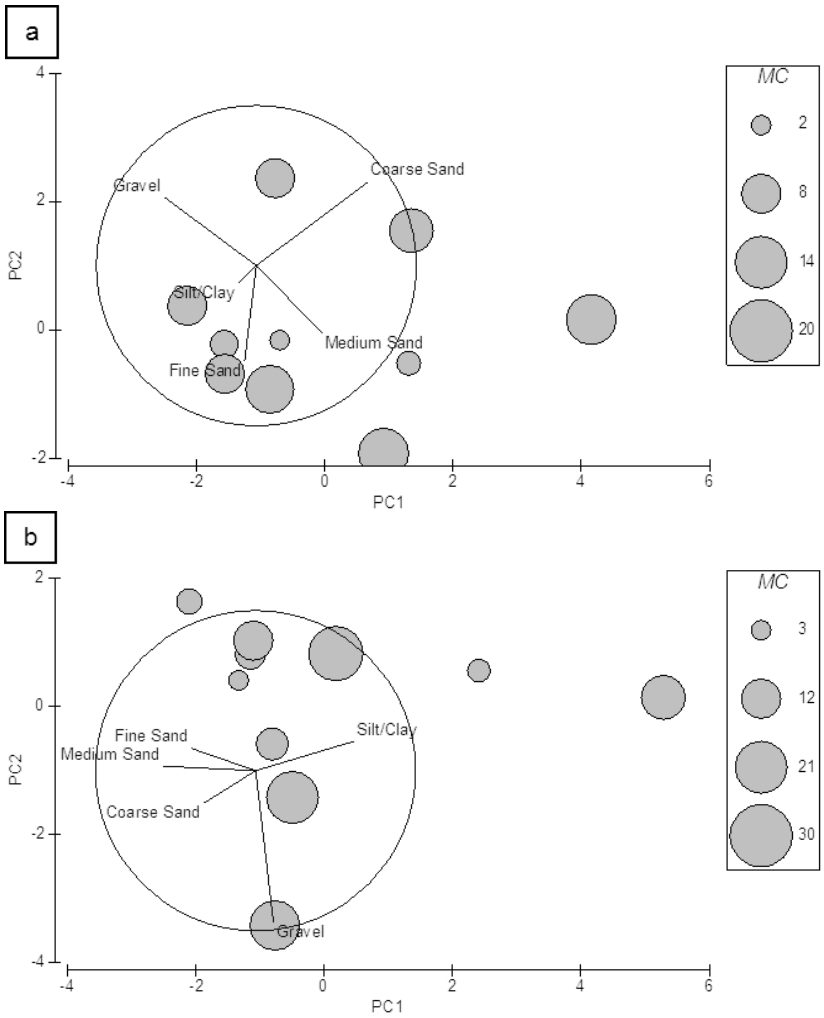

Figure 6.7. Principle component analysis (PCA) plots based on sediment particle size data with superimposed bubble plots for motile carnivores at the high dredging intensity site in a) 2001 and b) 2007.

6.4 Discussion

The classification of communities based on their functional attributes is a promising technique for assessing ecosystem function compared to the traditional approach that is based on taxonomic composition (Charvet et al., 2000; Bremner, et al., 2003; Gayraud et al., 2003; Botta-Dukat, 2005; Marchini et al., 2008). As pointed out by Bremner et al. (2003), any changes in ecological functions are more detectable using the traits approach than when based on the taxon. However, the function-based method can be more complicated as a result of trade-offs among the faunal attributes (Usseglio-polatera, 2000). Also, as discussed in previous chapters, several deficiencies, such as the lack of a complete database of the whole species list and possible inaccuracies in assigning functions to certain species, make it more complicated. Despite its weaknesses, the use of functional-based assessment can

still provide a better understanding of ecosystem function (e.g. Tilman et al., 1997; Hulot et al., 2000; Petchey and Gaston, 2002; Mason et al., 2005; Ricotta, 2005; Bremner et al., 2006; Lepš et al., 2006; Podani and Schmera, 2007; Schleuter et al., 2010;), and it also complements the use of structural analysis like the taxon-base (Cooper et al., 2008). Functions and characteristics of fauna are believed to be more relevant to the relationship between communities and the ecosystem(s) they inhabit compared to the species *per se* (Bengtsson, 1998; Bolam et al., 2002; Biles et al., 2003; Raffaelli et al., 2003). Similar functions could be performed by several different species of fauna, and the loss of a species performing a particular function may have no effect to the system as long as the loss is compensated by other species within the similar function (Walker, 1992). With this view, managing the ecosystem is perceived to be less challenging as maintaining functional groups is easier than conserving every species (Borja et al., 2000; Pavluk et al., 2000).

In Chapter 4, there are several indices presented for measuring ecosystem function based on the functional traits approach. While the indices are useful, there is no objective decision as to which index is better than the other. Hence, this chapter offers an alternative way by generalising the faunal classification without the use of excessive mathematical approaches, such as those required for the index calculations. The assessment based on feeding behaviours and mobility in the present study is believed to be the most significant to ecosystem function. These traits have been regarded as the central process in structuring benthic communities (Pearson and Rosenberg, 1978; Posey, 1987; Davidson et al., 2004). Studies in the English Channel and the North Sea recorded the importance of feeding and mobility as the primary characteristics which differentiate macrobenthic communities between stations (Bremner et al., 2003; Tillin et al., 2006; Marchini et al., 2008).It is however acknowledged that there are other mechanisms such as attachment and body form that are also significant in detecting the variability between communities (Bremner et al 2003). Whilst the limitation is acknowledged, the use of the simpler way in this study is to minimise the inaccuracy in assigning the species to traits without completely dismissing the functional mechanisms. Moreover, the way the organisms were classified in this study was also incorporated other important trait attachment although it is rather more subtle, for instance, the group sessile filter feeders also comprised of attachment species.

Area 222 was dominated by filter feeding fauna in both abundance and diversity. The domination was shown in particular, by the surface filter feeders group, which may have benefited from an unpredictable and inconsistent food supply (as an effect of disturbance). In contrast, deposit feeders prefer a more consistent food supply (Levinton, 1972). The abundance and diversity of filter feeders increased in 2007, when the area was considered to be less affected from disturbance, thus providing a more stable and predictable condition that should have favoured deposit feeders. However, this is not the case and may explain by the sediment characteristics in this area which was dominated by large particles such as gravel and coarse sand that may have created unsuitable conditions for deposit feeders. As pointed out by Hall (1994), the larger grain size means that more time is needed by the fauna to process an adequate amount of food. Dominance of filter feeders in the present study also accords with the different trophic structure recorded in the study by Barrio Froján (2005), where the area characterised by finer sediments was dominated by deposit feeding fauna. The composition of functional groups could be determined by the intra-specific interactions between members of the groups. These interactions can be direct, such as the high density of one group preventing the presence of another group. In the case of this study, the high density of sessile filter feeders might have prevented the suspended particulates from being deposited back onto the sediment, therefore reducing the food source for deposit feeders.

Sessile filter feeders were represented by the highest number of species, despite this group being highly competitive in food collection (Levinton, 1972). A possible explanation for this high diversity is that Area 222 is characterised by moderate current flow (Boyd, 2004), which enables a more thorough food distribution to take place in the filter feeders communities.

This study revealed that dredging had caused a shift in distribution of functional groups in Area 222. In the early years of this study period (particularly at the high dredging intensity site in 2002 and 2003), motile carnivores were the predominant group. Dredging activity might have destroyed natural shelter areas for most of the fauna through the removal of large sediment or through the burial of pits. This condition left the prey exposed, and subsequently attracted the motile carnivores from nearby areas: these motile carnivores then established themselves in the new feeding ground of the dredged area. Although there were some changes of

composition, the dominance of motile carnivores was not significantly different as compared to other functional groups or between years. This could be explained by the fact that the major impact of the dredging is the removal of fauna associated with the sediment (Newell et al., 1998) regardless of their functional groups. This consequence might have reduced the number of fauna from other groups that served as food for motile carnivores, and even reduced the number of this group itself. Another possible explanation is that predators (in this case motile carnivores) are usually represented by larger organisms compared to other groups (Cohen et al., 1993). As the larger species are characterised by having lower intrinsic rates of natural increase (Brey, 1999), the decrease of abundance of this group tends to occur at a faster rate compared to other groups at any given rate of mortality (Jennings et al., 2001). Therefore, the faster rate in the decline of this group may counter balance the loss of other groups to the point that the dominance of motile carnivores was not significant.

Multivariate analysis of the functional group distribution based on abundance and species richness revealed that the similarity exhibited by the sites is very much dependent on the dredging intensity. The more intense dredging had imposed a considerable degree of impact, since samples from the high intensity site were widely dispersed from the samples at the low intensity and reference sites. Some overlapping of the samples from the high intensity site with samples from the reference site suggested that there was movement towards recovery from the disturbance. This tendency towards recovery at the high intensity site was also evident from the reduction of ANOSIM R values. Meanwhile, at the low intensity site, the R values indicated that the recovery had already taken place in 2002; although recovery was not stable, since the values were significantly different in 2004 and 2007, and the later year recorded a lower R value. This difference may have been due to the substantial increase in sessile filter feeders at the low intensity site in 2004 which could be the result of intermediate disturbance (Connell, 1978; Roxburgh, 2004) or natural variability (Hewitt et al., 2001). The difference may also be due to the ANOSIM only measuring the difference between samples, without clarifying which sample is superior to the other.

Sessile filter feeders played a significant role in promoting the similarity between sites. This is not surprising considering this group, for most of the time, was the most

dominant, particularly at the low intensity and reference sites. With regard to this group alone, the high intensity site became comparable with the other two sites in 2007. In relation to the dredging activity, sessile filter feeders have returned to their original condition 11 years after dredging ceased. Since most of the sessile filter feeders in the present study were polychaetes which have higher intrinsic growth rates (Brey, 1999), they should, in theory, need less time to recover compared to other groups such as deposit feeders which are comprised of mostly crustaceans and molluscs. Nevertheless, this was not observed in the present study, possibly due to the sessile filter feeders' permanent attachment that making this group more likely to suffer most from the sediment extraction, yet take much longer to recover due to the disturbance to a stable sediment surface which was previously provided by the gravel. Understanding the role of filter feeders in the interaction of the community is important in helping future monitoring programmes and the production of dredging licences, especially if the abundance of sessile filter feeders will promote the occurrence of other groups, which is the case in this study.

The effect associated with sessile filter feeders is local habitat modification mainly due to the creation of biologically-mediated sedimentation around the fauna (Norkko, 2001), which in turn provides more optimal conditions for other groups. It also produces niche diversification that promotes a more diverse community (Downes et al., 2000). However, this view should be treated with caution as the increased number of species might be partially due to sessile filter feeding fauna having created a dense community, and therefore provided a greater chance of more species being collected (Downes et al., 2000). The increase of other groups parallel with the increase of sessile filter feeders, illustrates the important role of this group in attracting other species. Given that the sessile filter feeders were predominantly tube-building fauna, the results of this study are consistent with other studies that investigated the influence of structure-building fauna on the abundance and richness of the whole community (Woodin, 1978; Gallagher et al., 1983; Heck and Wilson, 1987; Trueblood, 1991; Callaway, 2006). Many studies concerning the effect of tube-building fauna on benthic community structure focus on specific species such as *Lanice conchilega* (e.g. Callaway, 2006; Rabaut, 2009). To the knowledge of the author, there is no such study that focused on *P. lamarcki*, but there are extensive studies reporting the effect of *Sabellaria* spp. on benthic community structure (e.g. Dubois et al., 2002; Pearce et al., 2007). Although both species create rigid tubes

that become bound together as also sharing the same feeding trait, it is uncertain that *P. lamarcki* might affect the composition of other infauna in the same way as *Sabellaria* spp. do. This is due to the fact that *Sabellaria* spp build reef-like platforms of tubes that create a new biogenic habitat for other species (Pearce et al., 2007), while this is not evident for *P. lamarcki* tube. Therefore, the association of sessile filter feeders (i.e. *P. lamarcki*) with the increase abundance of the whole community might be due to other factors such as the increase of organic materials (e.g. faeces).

Apart from their ability to change benthic community structure, filter feeding organisms in the present study were also important in supporting a quick recolonisation of the community after disturbance. According to Kenny and Rees (1996) a community dominated by fast growing *r*-selected species may be quicker to recolonise following physical disturbance, whilst a community dominated by *k*-selected species, which tend to have a much larger body size and be slow growing, take a longer time to recolonise. In the present study, some filter feeders that are considered as *r*-selected species showed their ability to quickly regain their dominance to the levels found before the disturbance took place. The recolonisation of the dominant *r*-selected species is seen as the main contributing factor to the recovery of a community from dredging impact. However, it is sensible to take into consideration their interactions with other species such as the less dominant *k*-selected species. For example, a study by Roberts (1979) found that a *k*-selected species, *Modiolus* spp. was able to alter the local environment by increasing the organic contents in the sediments through biodeposition although present in low number. This species also supports the presence of other species by providing shelter from predators, as well as supporting sessile filter feeders by providing a stable substratum for the sessile fauna to settle and grows (Roberts, 1979). Therefore, although the sessile filter feeders in the present study stimulated the community recolonisation, the importance of less dominant *k*-selected species should not be ignored.

Biotic interaction is not the only factor that relates to the modification of benthic communities. The results presented here suggest that grain size may also have an important role to play in explaining the similarity of functional traits composition between sites after a certain period of physical disturbance. The site which was most physically impacted had experienced a severe change in sediment size distribution,

and as a result, the distribution of trophic groups. As discussed above, sessile filter feeders were a characteristic group which dominated the area, whilst their presence promoted the return of other groups in the impacted area. In accord with the sediment distribution, this group tended to be associated with gravel rather than other finer particles. This is possibly due to the gravel providing a stable environment to the sessile filter feeder (Hall, 1994). Therefore, the loss of gravel may reduce the abundance of this group, and possibly have subsequent implications by losing other groups. Meanwhile an indirect impact could also happen through the loss of species associated with sessile filter feeders, such as species that shelter within the tubes. There is a consensus in marine aggregate dredging studies regarding the importance of gravel to lessen the impacts of physical disturbance on benthic communities (e.g. Newell et al., 1998; Boyd et al., 2003; Foden et al., 2009; Cooper et al., 2011) that are consistent with the findings of the present study.

The shift in sediment composition can also be related to the food availability for the filter feeding fauna. The food sources for filter feeders are varied as they feed on plankton, dissolved organic matter, organic aggregates and bacteria (Levinton, 1972). The food source might be abundant in muddy sediment in the form of large concentrations of bacteria that can be acquired from resuspended sediments. However, the presence of deposit feeders with their continuous activity of reworking sediments might reduce the stability of the sediments and hence tend to exclude the filter feeders (Levinton and Bambach 1970; Rhoads and Young, 1970). This might explain the low number of filter feeders at the High site in 2001 to 2004 as in 2001 and 2002, the sediment particles were generally finer than in 2007 (i.e. less gravel). The recovery of functional diversity in the present study is also in accord with the recovery of the ecosystem function (see Chapter 5) where it took place a few years after the recovery of the sediment composition occurred. This finding implies the importance of sediment composition, in particular the presence of gravel to promote the faunal recovery.

6.5 Conclusion

The main point that can be extracted from this chapter is the importance of sessile filter feeders sediment particles (gravel in particular) to provide appropriate environment conditions for the fauna, and subsequently encourage the recovery of the system. The interaction between benthic fauna and environment (as discussed in

this study) is an important finding to provide fundamental information with regard to the likely consequences of sediment disturbance on the benthic environment and its causative factor to aid recovery. In the context of marine aggregate dredging, this study is important in facilitating the management to mitigate the effects of dredging on ecosystem function, and is also important for the decision making of new dredging licences. Close association of the main group (sessile filter feeder) also provides useful information for the people within the dredging industry regarding the appropriate ratio of sand:gravel to be extracted so that the environment will not be severely damaged. The advantage of the use of multiple traits to understand benthic ecosystem function is acknowledged. The limited traits used in this study however, reduce the possibility of errors when applying traits to the species, and also reduces the 'noise' in statistical analysis which could appear from the use of many insignificant traits. With the support of traditional analyses (e.g. taxon-base analysis and abundance), this study could be a reliable method for the assessment and decision making in ecosystem management.

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Chapter 7: General discussion and conclusion

Summary of the main thesis questions:

1. Determine whether the recovery of the benthic system after dredging (based on traditional analysis) has occurred at the high intensity site within the study period *(Chapter 3).*

Hypothesis: Based on predictions in the previous studies, the recovery at the high intensity site would have taken place by 2007.
Half of the indices used indicated that no recovery had taken place within the study period. Therefore it is concluded that the prediction that the recovery at the high intensity site would occur 10 years after dredging stopped (2007) was inaccurate.

2. Determine the difference in recovery times of the benthic system based on both traditional and functional analyses (Chapter 3 and 4).

Hypothesis: Recovery based on functional analysis is faster than the traditional one.
The recovery based on traditional indices was slightly faster than based on functional indices. These findings were not in accord with the functional redundancy theory where the loss of one species will not affect the whole ecosystem function as long as the function lost is taken up by other species.

3. Identify any relationship between sediment particles and the biological recovery based on both traditional and functional analyses (Chapter 5).

Hypothesis: Gravel deposits provide a stable habitat for the macrofauna, therefore the presence of gravel promotes functional recovery.
Gravel deposits showed a strong association with the recovery of macrofauna based on different techniques. In addition, there was a strong association of gravel with the main characteristic species.

4. Identify if there are any trends of faunal recovery in term of the main functional groups (Chapter 6).

Hypothesis: The return of gravel deposits creates a favourable habitat for the recovery of sessile filter feeders.

Sessile filter feeders recorded a strong association with gravel, and this group also showed a strong influence on the recovery of the whole community.

7.1 Biological and physical recovery

Biological impacts of dredging on macrofaunal communities are usually associated with a reduction in the number of taxa, abundance and biomass (Newell et., 1998) as well as changing the community composition (Sánchez-Moyano, 2004). There are several factors which affect these processes, including the community types of the disturbed and unaffected areas (van Dalfsen et al., 2000), dredging intensity and penetration into substratum (Kaiser and Spencer, 1996), life cycles and feeding strategies (Lopez-Jamar et al., 1986) and the settlement of larvae and immigration of mobile species (Hall, 1994).

Previous studies in aggregate dredging areas suggested that the first stage of recolonisation is the settlement of a few opportunistic species that are able to take advantage of unstable sediments (Kenny and Rees, 1996; Desprez, 2000; van Dalfsen et al., 2000; Boyd et al., 2004). In the present study, the first species that recolonised the dredged area was *Pomatoceros lamarcki.* However, it might be a misleading to suggest that the recolonisation pattern in the present study was in accord with the studies mentioned above. This is due to uncertainty as to whether *P. lamarcki* should be classified as an opportunist or a *k*-selected species (Claveleau and Desprez, 2009; but see Gray and Elliott, 2009). If it is assumed that *P. lamarcki* is a *k*-selected species, the dominance of this species at the low intensity site may reflect that the initial recolonisation stage at this site that has already taken place for some time; hence a *k*-selected species became dominant. In contrast, its dominance at the high intensity site might reflect errors in sampling; with some samples being collected from the undisturbed seabed with high proportion of gravel (*P. lamarcki* recorded a strong association with gravel deposit – in Chapter 5).

The biological status of a disturbed area was assessed using traditional analyses where the community within an impacted site was compared to either an undisturbed reference area or the community prior to a disturbance (Cooper et al., 2007) if data exists. The indices used in traditional analyses are only taking into account the

assemblage structure incorporating basic measurements such as abundance, biomass and species richness. The present study showed a clear difference in term of faunal structure between dredged and undisturbed sites (Chapter 3). This was the results of direct removal of the fauna (together with the sediment), emigration of species and increased likelihood of injury and death due to the impact of physical disturbance. However, the impact of dredging in changing the macrofaunal community was only obvious when this activity was carried out at high intensity. No obvious change was recorded to the community within the area subjected to a much lower dredging intensity. Instead, there were certain cases, especially in 2004, where several indices such as abundance and biomass recorded a much higher value compared to the community before dredging took place. The elevated values recorded in the site with lower dredging intensity were perhaps due to the successional changes which were still going on. The other possibility was the impact of medium disturbance may have promoted a more 'healthy' community than the original condition (Dial and Roughgarden, 1998). Based on this theory (Intermediate Disturbance Hypothesis), it is suggested that disturbance might have increased the carrying capacity of the system, hence more individuals can be accommodated; and also might create a system where a greater variety of species can coexist. The site exposed to high dredging intensity not only recorded a different community structure compared to the original condition, but was also characterised by high variation within the site. This may be because the frequent disturbance on the seabed surface had created denser areas of furrows which are more likely to accommodate different faunal communities, increasing system heterogeneity. This in turn increased the possibility that samples were collected from patches of high and low abundances.

A more recent way of assessing the biological status of an ecosystem is by using functional analyses. While the traditional method only incorporates the structure of community, the functional analyses take into account the biological and ecological characteristics of the community. As for the community structure, the change caused by dredging activity on functional diversity was also more obvious at the site with high intensity of dredging. As a result of 'functional redundancy' (see section 4.1), functional diversity at the high intensity site was expected to be less dissimilar to reference sites than the dissimilarity recorded based on traditional indices. However, this is not the case for most of the functional indices where results show no obvious trend of faster recovery using functional traits approach. A possible explanation is, at

the high intensity site, the high level of disturbance had removed many species and individuals, and the species remaining could not make up for the functional capacity of the lost species. Perhaps, if dredging intensity was more moderate, the species remaining after dredging could preserve as much functional diversity as it in the undisturbed site.

The period of time needed for biological recovery varies depending on the method of assessment used. The recovery at the high intensity site showed varied timescales using both traditional and functional methods, with differences of more than 5 years (Table 7.1). Recovery times were more consistent at the low intensity site, with only one to two years difference between all the analyses. Traditional analysis recorded a more consistent result with all except N suggesting a recovery at the low intensity site as early as 2001, or five years after the dredging terminated. Functional analyses recorded rather different recovery times, with ITI and BTA recorded the longest time (7 years after dredging ceased).

Table 7.1. Recovery times at the high and low dredging intensity sites based on the different analyses.

Index	Year of recovery (Number of year after dredging)	
	Low intensity site	High intensity site
Abundance (N)	2002 (6)	2007 (11)
Biomass-AFDW (B)	≤ 2001 (≤ 5)	> 2007 (> 11)
Richness (S)	≤ 2001 (≤ 5)	> 2007 (> 11)
Margalef (*Dm*)	≤ 2001 (≤ 5)	> 2007 (> 11)
Simpson (*Ds*)	≤ 2001 (≤ 5)	≤ 2001 (≤ 5)
Taxonomic Distinctness (TD)	≤ 2001 (≤ 5)	2002 (6)
Somatic Production (Ps)	2002 (6)	> 2007 (> 11)
Infaunal Trophic Index (ITI)	2003 (7)	> 2007 (> 11)
Biological Traits Analysis (BTA)	2003 (7)	> 2007 (> 11)
Rao's Quadratic Entropy (Rao's Q)	≤ 2001 (≤ 5)	≤ 2001 (≤ 5)
Functional Diversity (FD)	≤ 2001 (≤ 5)	> 2007 (> 11)

Macrofaunal communities in this study recorded a faster recovery (or at least progress towards recovery) at the low intensity site than at the high intensity site. In the case of the high intensity site, this might be due to a greater shift of sediment composition as a result of greater dredging intensity; hence it needed a longer period to return to its original state. This site had a finer sediment particle size (i.e. lower percentage of gravel and higher percentage of coarse sand) compared to the low intensity and reference sites during the early period of investigation, but the sediment

proportions became fairly similar to from 2004 to 2007 (Figure 5.2). At the low intensity site, the percentage of gravel (which had a positive correlation with the assemblage structure) had returned to the same composition as the reference sites before this study commenced, and this early physical recovery has promoted an early biological recovery. Conversely, the high intensity site had a low percentage of gravel, but a higher percentage of coarse sand as compared to the reference site. As this proportion is now becoming similar (2004 and 2007), it might be suggested that physical recovery was almost complete in 2007, so that biologically recovery can now take place over the next few years. The topography at the high intensity site was still suffering from the impact of the dredger draghead where dredge tracks were still visible using side scan sonar (Cooper et al., 2005). The reliance of biological recovery on the physical aspects of the seabed has been suggested in many studies (e.g. van Dalfsen et al., 2000; Robinson et al., 2005; Cooper et al., 2008; Foden et al., 2009; Desprez et al., 2010) where recolonisation of similar macrofaunal assemblage is more likely to happen if there is no difference of sediment characteristics, topography and hydrodynamic regime between before and after disturbance.

The period of time (between 5 and11 years) needed for recovery in the present study differs from other studies involving physical disturbance (e.g. Powilleit et al., 2006; Simonini et al., 2007; Wilber et al., 2007; Borja et al., 2009), which in general took only 2 – 4 years. However, these studies were conducted in areas with a one-off disturbance with no 'legacy' stressor (Borja et al., 2010). In contrast, Area 222 in the present study was continuously dredged for 25 years; hence the physical change of the seabed was expected. For example, there is evidence of dredge depressions resulting from static suction hopper dredger (Cooper et al., 2005). By comparison to other dredging areas in the North Sea, Area 222 appeared to be impacted for a longer period in term of seabed topography. This leads to the conclusion that this phenomenon was due to the characteristic of this area which is classified as 'low energy', which in turn requires many years or possibly decades for its seabed to return to conditions similar to the pre-dredged state (Boyd et al., 2004). This type of impact is likely to prolong the recovery of the macrofaunal communities. Elliott et al. (2007) pointed out that the trajectory of degradation may be different from the trajectory of recovery. Therefore in the case of the present study, the time taken for the system to recover could be longer than the time taken to degrade the system.

Foden et al. (2009) compared recovery rates of dredging areas around UK and they found out that a faster recovery occurred in areas with strong tidal stress and highly mobile sands. Physical features in Area 222, which was characterised by weak-moderate tidal stress and medium/coarse sand are believed to extend the recovery in present study.

7.2 Traditional or functional analyses?

Despite the consistency showed by traditional analyses, it might be unwise to suggest this technique is more suitable than functional techniques for assessing recovery. This consistency might be due to the traditional analyses (S, *Dm*, *Ds*, *J'*) using a similar mathematical basis (i.e. number of species). Therefore it is unsurprising if these analyses produced a similar recovery period as opposed to functional analyses, which use a different basis, and hence produced different recovery times. Moreover, both traditional and functional techniques might give a different perception to stakeholders on the recovery of organisms. Although traditional techniques are only based on the presence and relative abundance of species without taking into account their biological and ecological roles, however, they are fundamental as far as biodiversity is concerned. For instance, people who are interested in biodiversity of an area might want to know that the area can still accommodate as many species and individuals after disturbance, regardless of their functional value. After all, if the whole community recovers, its functional capacity would also be recovered. It has been argued in many studies that communities with greater diversity are normally associated with a greater resilience to stresses, thus increase the stability of ecosystem processes (e.g. McCann, 2000; Loreau et al., 2001; Hooper et al., 2005). However, some conflicting results have been recorded in empirical and theoretical studies (Ives and Carpenter, 2007). Moreover, recovery based on species diversity and assemblage may be unlikely due to the nature of the seabed ecosystem which constantly changes (see section 4.1). Therefore, measurements using functional diversity merit further consideration. In this case, the community after disturbance may not be similar to the reference site, but still maintain the same ecosystem function. Functional analysis is also considered to be more suitable to measure ecosystem productivity and vulnerability (Tilman, 1997, Hulot et al., 2000, Diaz and Cabido, 2001). Although it shows great potential, assessing the ecological status of a community using functional analysis could be problematic. Not only there are many different functional traits to choose from and assign to every

species, the approaches in calculating the functional diversity are also different. Clearly, the complexity in measuring functional diversity makes it more prone to variation as compared to the traditional species diversity. There are no generally accepted complete lists of traits, thereby necessitating considerable effort in assigning missing entries.

7.3 Animal-sediment relationship

The relationship between macrofauna and sediments is based on several factors; through life history development (Walsh, 1993), mobility (Chia et al., 1983), life habit (Bachalet et al., 1992) and feeding mechanisms (Lindsay and Woodin, 1995). Understanding the interaction between organism and sediments is important as it helps in identifying the types of sediments that are favoured by the organism (Constable, 1999), and this has the subsequent relevance to the dredging activity where the sediments are constantly change through disturbance and local hydrodynamic.

The present study showed that gravel deposits had a significant influence in the composition and distribution of macrofauna. Recovery of macrofaunal assemblages and ecosystem function took place at a faster rate at the sites with a dominant gravel fraction. This may be explained by the role of gravel in providing a stable habitat to promote faunal recolonisation and recovery. However, high proportion of gravel in Area 222 could also create another problem. Results from the present study with regard to the distribution of main characteristic species which are strongly associated with gravel deposit suggest that the gravel-dominated habitat is more susceptible to physical and biological changes (Cooper et al., 2011).

7.4 Application for marine management

According to Fisher et al (2009), the ecosystem processes and functions can generally be classified based around intermediate and final services which associated with indirect and direct benefits respectively. Atkins et al. (2011) suggested the intermediate services are better termed as ‘fundamental services’, which are classified as the bottom-up physico-chemical processes that create the fundamental ecological niches for the organisms to colonise (Figure 7.1). This process is referred to as the ‘environment-biology’ relationship (Gray and Elliott, 2009). Under these ecological niches, the ‘final services’ are set up through the

interaction within the communities which is termed as the 'biology-biology relationships (e.g. predator-prey and competition), and the modification of the environment ('biology-environment' relationships) through processes such as bioturbation and organic removal (Gray and Elliott, 2009; Atkins et al., 2011). An ecological system that provides a complete suite of functions in terms of both physic-chemical and biological aspects will produce benefits to society – i.e. Ecosystem Services and Societal Benefits (ES&SB). The concept of ES&SB provides a fundamental link in delivering those benefits to society as shown in DPSIR framework (see paragraph below) (Atkins et al., 2011).

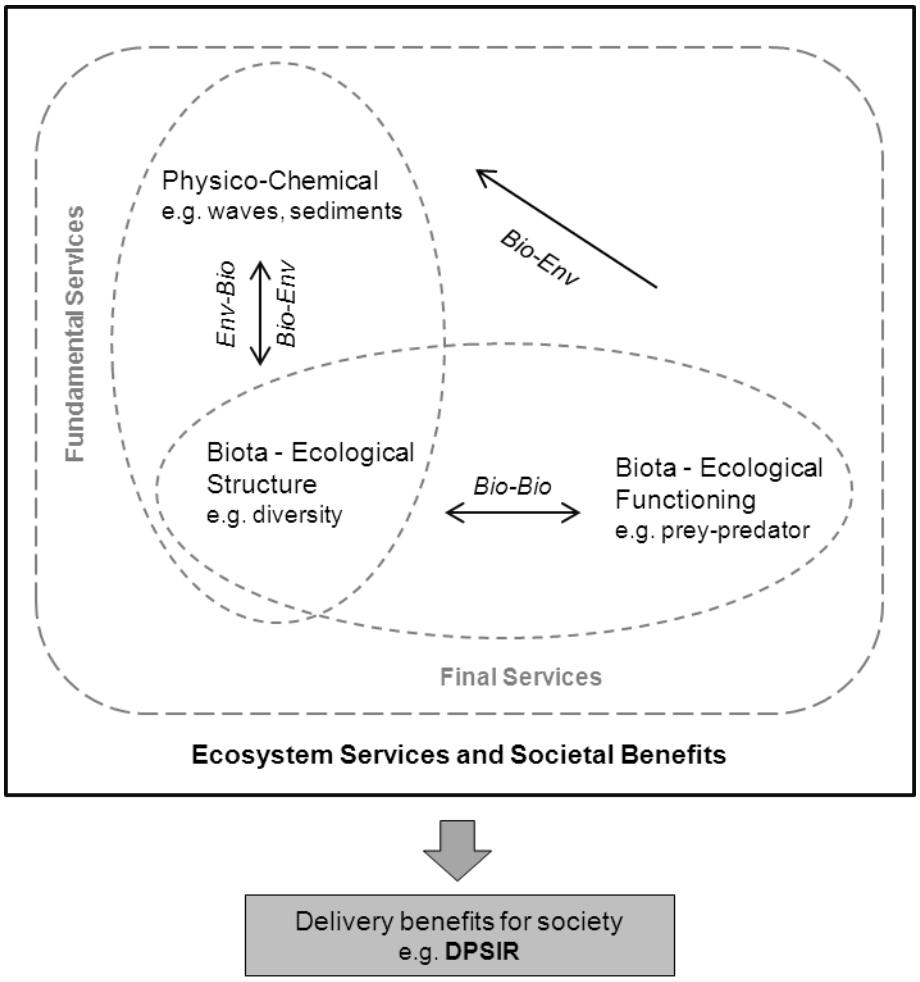

Figure 8.1. The ecosystem services that provide a fundamental link in providing benefits for society. Adapted from Atkins et al., 2011.

Due to its highly complex system, the study and management of the marine environment requires a solid understanding of its structure and function. There is also the need to developing tools for this management where a better communication

between the scientific community and environmental managers can be generated. The increasing requirement of understanding marine environment and its link with the socio-economic impacts are shown in the increasing application of DPSIR approach (Elliott, 2002). The first aspect required to be understood is the DRIVERS of change (e.g. the increased requirement for aggregate extraction). The dredging activity creates subsequent PRESSURES to the marine system. Therefore it is important in the management view to determine the STATE CHANGE of the physical, chemical and biological aspects of the system. Appropriate monitoring procedures and the use of indicators of change are required to understand the IMPACTS. Finally, human RESPONSE is needed to implement any changes needed. In the case of marine aggregate dredging, human response to this activity is the use of good practice and the application of some limits, for example a dredging licence with a specific intensity of activity, with or without screening, may be allowed. Considering the above, it is very important for the scientific community to ensure the knowledge about the complexity of the marine system, the effect of dredging activity and the responses at different levels of the system is explained and demonstrated to the people in dredging industry, environmental managers and politicians (Elliott, 2002).

The approach used in this study is one of understanding the impacts of human activity on a marine ecosystem. The impact (I) component of DPSIR requires that the assessment of an ecosystem has to be based on appropriate indices to aid in providing a decent interpretation (Borja and Dauer, 2008). The subsequent response (R) can be implemented in order to manage the ecosystem (Figure 7.2). As the marine environment is very complex, monitoring its status in a specific area over a long-term period very important as a reference in assessing or predicting the impacts in other area. Additionally, this can also be used as a baseline reference for the licencing new areas or allowing the continuation of dredging in a licenced area. At the moment, there are limited studies on the impact following a sustained dredging phase over a long period of time. Most of the previous studies concern the impacts on the basic community structure with little emphasise on the overall functionality of the ecosystem. The approach in the present study where assessment of the impacts was based on multiple measures (structurally or functionally) is one way of disseminating the output to different bodies such (e.g. dredging companies and policy makers) with different interests and concerns.

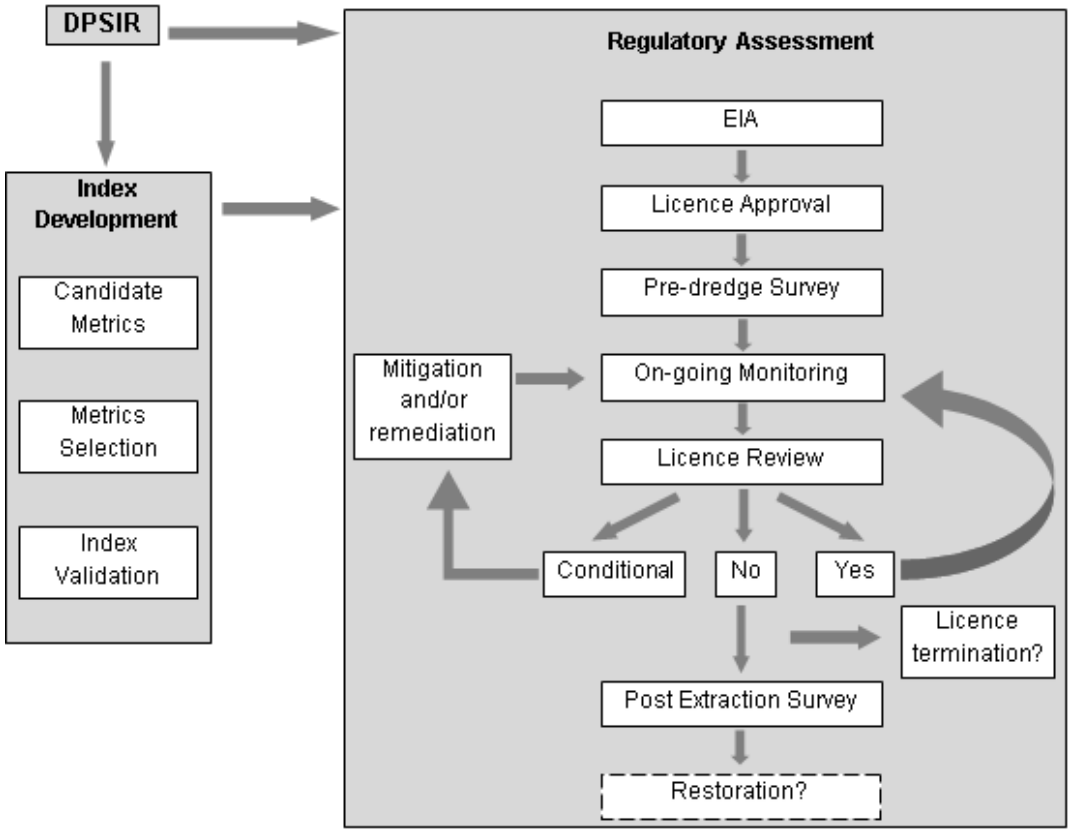

Figure 7.2. The application of DPSIR framework for the index development and licencing assessment. Adapted with modifications from Atkins et al., 2011 and Ware and Kenny, 2011.

7.5 Limitation of the study and recommendation for future works

The use of indices that quantify the status of macrofaunal community in terms of structural and functional features provide a better step in achieving improved understanding of changes in ecosystem function following disturbance by aggregate dredging. The long term sampling regime applied in this study might also be useful in understanding the variation of ecosystem dynamics which is an important consideration when determining recovery status. There are, however, several limitation identified in this study. Firstly, the unavailability data in 2005 and 2006 created a gap in terms of following successional changes, particularly at the low intensity site. The second limitation was the lack of other physical data (acoustic and seabed imaging) which made the attempt to relate the macrofaunal community with specific sediment particles fairly difficult. In addition, one might argue the use of too many indices might add the complexity to the judgement. However, it was the aim of this study to make a comprehensive assessment using different indices with different characteristics. This difference was also the reason why the present study did not

attempt to combine multiple indices (i.e. multi-metric analysis) for an easier interpretation

Based on the limitations discussed, it is recommended that the future works concerning system recovery should be carried out for a longer time series as well as with multiple physical parameters (e.g. seabed topography, hydrodynamic, organic contents) to support the biological data. However, it is acknowledged that this depends on the financial status of the project. It is also suggested that, for future works, some functional indices (e.g. BTA, FD and Rao's) can be further analysed. Chapter 6 in the present study describes an initial attempt for a more detailed assessment based on multiple traits. A similar approach based on the traits in BTA, FD and Rao's Q would be an interesting appraoch in understanding species characteristics and interactions that are the central factors of recovery.

7.6 Conclusion

Studies on the impact of human induced activities on ecosystems have been carried out extensively and will need to continue as such activities are increasingly vital for socio-economic gain. Different studies reported different levels of impact on ecosystem and this could be due to both intrinsic and extrinsic factors. Studies carried out in different areas suggest different responses of benthic fauna on habitat disturbance. This thesis provides a site-specific insight to the impact of physical disturbance on benthic ecosystem function through dredging activity. The use of various measurements does not simply complicate the interpretation of environmental status. Instead, multiple indices are useful indicators to assess the ecosystem based on different perspectives and purposes. The thesis also provides evidence that higher levels of physical disturbance impose greater damage to the ecosystem. The discrepancy of the findings at the high dredging intensity site in the present study with the prediction of recovery in previous studies by Boyd et al. (2004) and Cooper et al. (2005) demonstrate the importance of monitoring the impact for a longer period. This information is valuable as a reference for the environmental managers and policy makers when it comes to making decisions with regard to activities that damaging benthic habitat.

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Appendix 1

The influence of *Hediste diversicolor* on sediment stability: a mesocosm study

Introduction

The stability of cohesive sediments depends on their characteristics (Dade et al., 1992) and the physical and biological interactions within the sediments (Paterson, 1997; Paterson et al., 2000; Black et al., 1998). The characteristics and interactions of the sediments can lead to its relative stabilisation or destabilisation (Widdows and Brinsley, 2002) through the activities of some key organisms (de Brouwer et al., 2000; Widdows et al., 2000a; Herman et al., 2001).

Hediste diversicolor (recently accepted name of *Nereis diversicolor* (Read and Fauchald, 2011)) is one of the key species that impacts on the sediment stability. This species, which is common in estuarine ecosystems in Scotland, is a burrowing organism that constructs complex gallery networks to depths of up to 30 cm, depending on its body length, with the larger organisms or more than 10 cm length can be found in the upper 2-3 cm (Esselink and Zwarts, 1989; Fernandes et al., 2006). Burrowing activity by *H. diversicolor* has a direct impact on the ecosystem due to sediment reworking that ensures the transport of oxygen from the surface to the deeper layers (Biles, 2002, Mazik et al., 2008), which may develop the vertical and horizontal redox gradient (Mazik et al., 2008). The presence of burrows also increases the chemical exchange process at the sediment-water interface (Mazik et al., 2008). Other than a burrowing activity, its variety of feeding mechanisms, namely filter and deposit feeding, scavenging and predation (Esselink and Zwarts, 1989), also have different effects on sediment characteristics. As a result of its ability to change feeding methods, and adapt its behaviour to environmental changes, *H. diversicolor* has *become* one of the most common species in intertidal areas in North Western Europe (Green, 1968). Although it has been widely studied, there is no consensus achieved as to whether to consider this species as a stabiliser (e.g. Meadows and Tait, 1989; Meadows et al., 1990) or a destabiliser (e.g. de Deckere et al., 2001; Widdows et al., 2006). Fernandes et al. (2006) also revealed that the effect of *H. diversicolor* on sediment stability was ambiguous where stabilising effect

exerted by this species was recorded under low current velocity when its gallery building activities enhance lateral compaction; whereas under high current velocity, this species created a destabilising effect as the erosion process in mucus-stabilised sediments was at a faster rate than in unbound sediments (Luckenbach, 1986).

So far, most of the studies on *H. diversicolor* have focused on the different effects its density and biomass imposes on sediment stability (e.g. Mazik and Elliott, 2000; Fernandes et al., 2006). It is believed no existing study has been conducted to determine the effect of different body lengths on sediment stability. The main objectives of the present study were therefore to 1) determine the effect of *H. diversicolor* on sediment stability; 2) quantify if this effect was in any way influenced by the body length of this species; and 3) examine whether different seabed conditions affect the (de)stabilising capacity of *H. diversicolor*. To achieve this, a group of *H. diversicolor* with different body lengths were studied in mesocosms to determine their effect on sediment properties such as organic content, colloidal carbohydrates, colloidal proteins, chlorophyll *a* and the microphytobenthos assemblages. The focus on the body length was based on the hypothesis that an assemblage with small-bodied organisms has a different effect on sediment stability compared to an assemblage with large-bodied organisms. This mechanism might have important consequences following anthropogenic disturbances that would remove mostly larger organisms from the sediment. While recovery of the area might result in a recovery of the species biomass, the change in body size distribution might result in a change in the effects the species has on the sediment reworking and hence result in a different stability of that area. In the context of ecosystem function, the different body sizes can be related to different metabolic rates by the organism and their responses to the environment (e.g. nutrient transport), which subsequently will affect the functionality of the system. Moreover, the body size is also deemed to be an important trait as it influences population abundance, life history adaptation and species interaction (Fisher et al., 2010).

Methods

Sample collection and preparation

Samples were collected from the intertidal mudflats on the Eden Estuary, Scotland, between 15 December 2010 and 18 February 2011. The sediment was transported to the laboratory and sieved through 0.5 cm mesh screen to remove the macrofauna. The sediment was completely defaunated by freezing for 48 hours. The defrosted sediment was homogenised and transferred into 8 mesocosm tanks (20 cm diameter, 25 cm deep) to a depth of 12 cm (3.8 L). Each tank was filled with pre-filtered (63 µm) seawater, aerated and left for 48 hours to equilibrate. Following the 48 hours, the water was carefully drained and fresh biofilm (~5 mm, in the form of slurry solution) was added on top of the sediments. The biofilm was collected from the top ~2 mm of the sediment surface from the same site and sieved through 0.5 mesh screen to exclude any macrofauna. All tanks were left under lights in a 10°C room for another 48 hours to ensure the establishment of the biofilm (Figure 1a). Pre-filtered seawater was carefully added to the mesocosms followed by populations of *H. diversicolor,* which were then acclimatised for 48 hours. All tanks were aerated under day/night condition mimicking the natural conditions (i.e. light on from 0830 – 1600 hours) (Figure 1b).

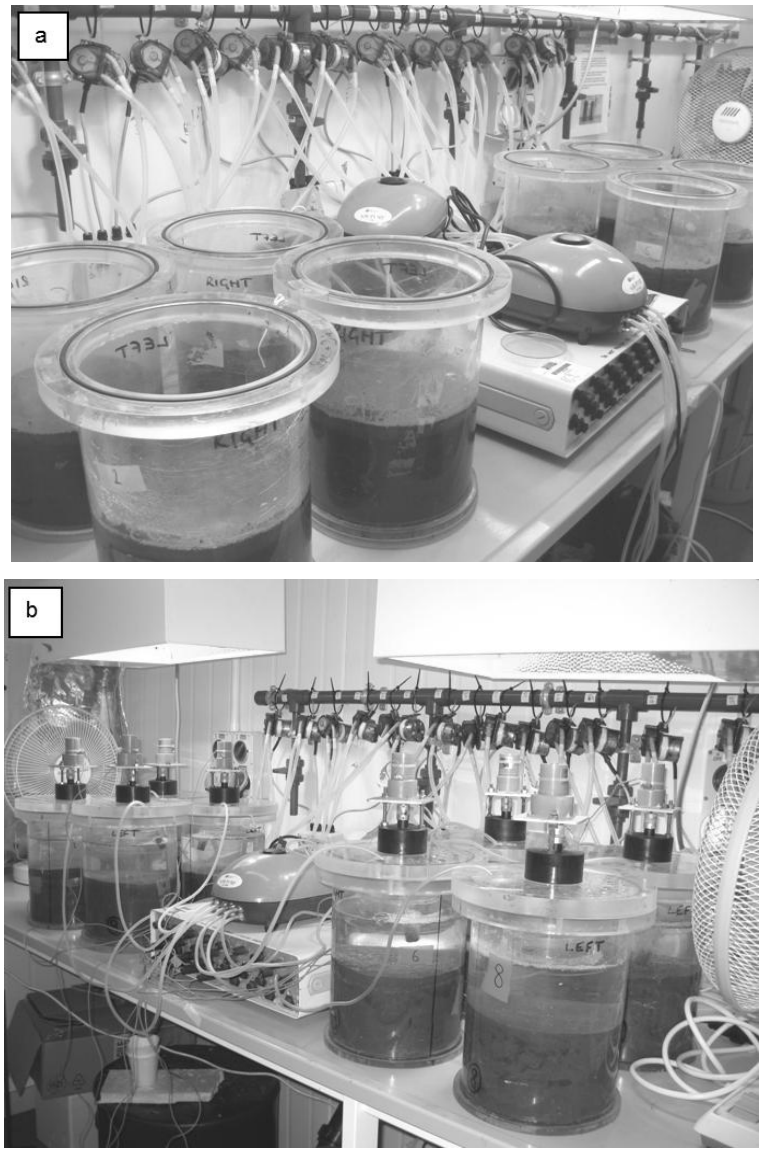

Figure 1. Experimental set-up of a) the development of biofilm under light condition, when water is drained from the tanks and b) introduction of worms in treatment tanks, with tanks filled with aerated seawater.

Experimental set-up and sampling strategy

Three treatments were established respectively for three different size classes, namely treatment S (small-bodied *H. diversicolor*: < 5 cm), treatment M (5-10 cm) and treatment L (> 10 cm). Biomass of all treatments was normalised to 4 g which represents the natural biomass of this species in Eden estuary (Biles, 2002). Additionally, a control treatment contained no organisms but was otherwise identical. For all tanks, a constant flow rate of 21 cm^{-s} (the minimum flow produced by the mesocosms) was set throughout the experiment using a revolving skirt (12 cm diameter) located at the top of the tank. Due to the limited number of tanks, the

experiment was carried out in batches of 2 replicates a time. Repetition was carried out to obtain 4 replicates. The whole experiment was also repeated (4 replicates) at a higher flow rate of 45 cm^{-s} where sediment erosion was observed. The erosion condition was determined based on the turbidity measured using a Cohesive Strength Meter (CSM). A schematic detail of the experimental setup is shown (Figure 2). For each replication under both flow conditions, sampling started 48 hours after the organisms were introduced in the tanks, and carried out every day for 4 days (Day 1 – Day 4).

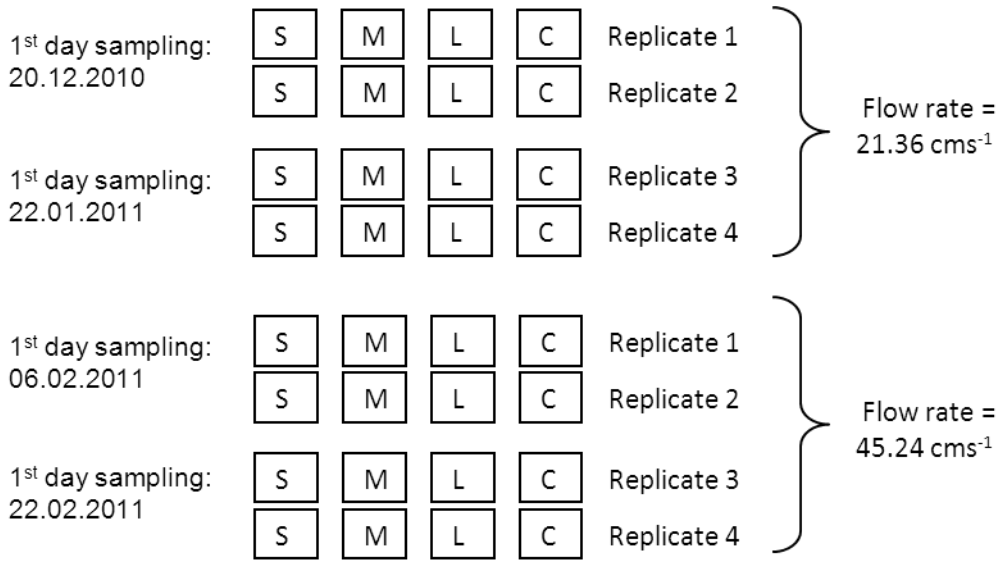

Figure 2. Schematic diagram of experimental set-up and sampling strategy. Rectangular blocks with the letters S, M, L and C represent the tanks of treatments S, M and L, and Control tank respectively.

Laboratory sample collection

Sediment samples for organic content analysis of each experimental unit were collected from ~5 mm sediment surface using a small aluminium plate (2 cm x 1.5 cm). Samples were dried in an oven at 50°C for at least 48 hours before the analysis was carried out. Using the same aluminium plate, a ~5 mm sediment surface was collected for Low Temperature Scanning Electron Microscope (LTSEM) analysis (Paterson, 1995). The sediment was immediately frozen in liquid nitrogen. The frozen sediments were then kept at -20°C for later analysis.

A mini core (D = 10 mm) was used to take surface sediment samples from the experimental tanks for the remaining analyses. The collection was made by the following steps (Figure 3): 1) the core was placed into the sediment and the upper 5 - 10 mm layer was removed; 2) syringe-plunger was pushed to exclude any excess sediment in order to keep only the surface (2 mm) of the sediment; 3) the sediment cores were immediately frozen with liquid nitrogen; 4) the frozen samples were extracted from the syringe, wrapped in labelled aluminium foil and stored at -80°C for later analyses. Meanwhile the sediment cores for bulk density analysis were transferred to labelled plastic bags (n = 5) and kept frozen at -20°C.

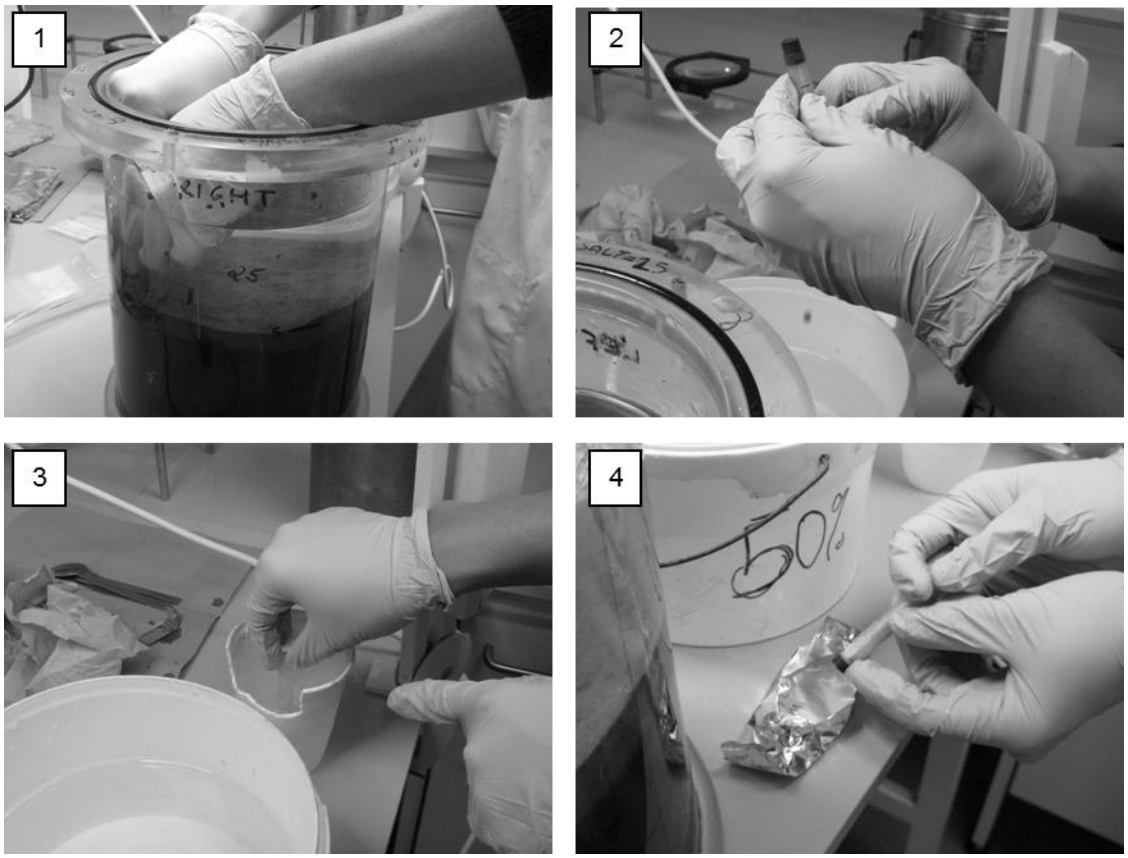

Figure 3. Sample collection using mini core.

Laboratory sample analysis

Organic content

Analysis of the organic content in the sediment was based on techniques outlined in the HIMOM protocols (2005). A sub sample (~ 2g) of oven dried sediment was grounded into a fine powder and then added to a pre-weighed crucible. The sediment

and crucible were then weighed to obtain the sediment dry weight and then placed in a muffle furnace for 4 hours at 450°C. A desiccator was used to allow the sediment to cool whilst preventing the absorption of moisture from the atmosphere. The cooled sediment and crucible were reweighed to determine the organic content using Eq. 1:

Organic content (%) =

$$100 - \left(\frac{\text{Crucible and sediment after ignation (g) - crucible (g)}}{\text{Crucible and sediment before ignation (g) - crucible (g)}} \right) x\,100 \qquad \text{Eq. 1}$$

Colloidal carbohydrate analysis

Two millilitres of distilled water were added to safety-lock Eppendorf caps containing mini core samples. Once the samples had defrosted (~15 min), the samples were mixed for 1.5 h using a horizontal mixer. The mixed samples were then centrifuged at 2500 rpm for 15 min. Approximately 1 ml of the supernatant was removed into a new Eppendorf tube and separated in triplicates of 200 µl (another ~1 ml of the supernatant was taken for protein analysis, but with 250 µl triplicates – see section below). The 200 µl samples were analysed following the Dubois Assay (Dubois et al., 1956). 200 µl of phenol (5%) and 1 ml sulphuric acid (98%) were added to the samples. The samples were then vortexed and left for 35 min in a water bath at 30°C after which the absorption was read at 488 nm wavelength in a Cecil 3000 spectrophotometer. The carbohydrate concentration was calculated from a glucose standard curve, which was prepared beforehand. For the preparation of the glucose standard, a selection of glucose solutions ranging from 0, 20, 50, 100, 125, 150, and 200 µg ml^{-1} were measured (Lubarsky, 2011). The absorbance of these solutions was used to construct a standard curve from which the calibration equation was obtained by linear regression (Eq. 2).

$$y = Mx + C \qquad \text{Eq. 2}$$

where, y = glucose absorbance, M = gradient, x = glucose concentration, C = intercept on the axis. Linear regression of the standard curve was used to obtain the coefficients and constants of colloidal carbohydrate using the following equation:

$$\text{Colloidal carbohydrate } (\mu g\ cm^{-3}) = \frac{(Abs - B) - C}{M} X\ 4 \qquad \text{Eq. 3}$$

where, Abs = sample absorbance, B = absorbance of blank sample with zero glucose concentration, C = intercept of the glucose standard line, M = gradient of the line. The factor of 4 was applied to account for the sample dilution in water, where 0.5 cm^3 of samples diluted in 2 ml of water (Lubarsky, 2011).

Colloidal protein analysis

Five chemical reagents were prepared for protein analysis:

Reagent 1: 143 mM NaOH, 270 mM Na_2CO_3,

Reagent 2: 57 mM $CuSO_4$,

Reagent 3: 124 mM Na-tatrate,

Reagent 4: a mixture of Reagents 1-3 in a ratio of 100:1:1,

Reagent 5: Folin reagent diluted with distilled water of 5:6.

Triplicate samples of 250 µl of the supernatant from the mini-core samples (prepared as described in section 7.2.4.2) were mixed with 250 µl of 2% sodium dodecyl sulphate (SDS) and 700 µl of Reagent 4, vortexed and then incubated for 15 min at 30°C in a water bath. Reagent 5 was added to the samples before a further incubation for 45 min. The absorption was measured at 750 nm wavelength in a Cecil 3000 spectrophotometer (Raunkjaer et al., 1994; Gerbersdorf et al., 2008). A calibration curve was produced from a BSA standard (Bovine Serum Albumin, 10 g) to calculate the protein concentrations. Standard was made within a range of 0, 20, 50, 125, 150, 200 and 250 µg ml^{-1} from a 200 mg l^{-1} BSA stock solution. A standard curve was constructed as in the calculation for colloidal carbohydrates (Eq. 2). Based on the standard curve, the coefficients and constants of colloidal protein were obtained from the following equation:

$$\text{Colloidal protein } (\mu g\ cm^{-3}) = \frac{(Abs - B) - C}{M} X\ 4 \qquad \text{Eq. 4}$$

where, Abs = sample absorbance, B = absorbance of blank sample with zero BSA concentration, C = intercept of the standard line, M = gradient of the line. The factor of 4 is applied to account for the sample dilution in water, where 0.5 cm^3 of samples diluted in 2 ml of water (Lubarsky, 2011).

Chlorophyll a content

Pigment extraction for chlorophyll *a* analysis was based on the HIMOM protocols (2005) and carried out under dim light while samples and solvent were kept cold. Small amounts of sediment (10-50 mg) from mini core samples were placed into pre-weighed Eppendorf tube into which 1ml of acetone (90% buffered with 10% saturated sodium carbonate) was added, and re-weighed. The samples were placed in a sonicator containing -4°C seawater for 90 min. Samples were then kept frozen at -20°C for 48 hours (interspersed with vortexing after 24 hours) and then centrifuged for 3 min at 1300 rpm. The extracted pigments were decanted in a 1 cm cuvette and absorbances were read at 630, 647, 664 and 750 nm in a spectrophotometer. Chlorophyll *a* content per sample was calculated using Eq. 5

Chlorophyll *a* ($\mu g\ g^{-1}$) =

$$\frac{[11.85(E_{664} - E_{750}) - 1.54(E_{647} - E_{750}) - 0.08(E_{630} - E_{750})]}{\text{Weight of sample (g)}} \times V_e \qquad \text{Eq. 5}$$

where, E = absorbance at given wave lengths, V_e = extraction volume (ml).

Water content and dry bulk density

The methods for measuring water content and dry bulk density are integrated together and calculation followed the protocols in HIMOM (2005). The frozen samples were weighed. The sample was freeze-dried for at least 24 hours to remove any water and then re-weighed. Calculation of water content was obtained using Eq. 6 while the dry bulk density was calculated using Eq. 7.

Water content (%) =

$$\frac{\text{Wet sediment (g)} - \text{Freeze dried sediment (g)}}{\text{Wet sediment (g)}} \times 100 \qquad \text{Eq. 6}$$

Dry bulk density ($g\ cm^{-3}$) =

$$\frac{\text{Wet sediment (g)}}{\text{Volume } (cm^{-3})} \qquad \text{Eq. 7}$$

Magnetic Particle Induction (MagPI)

The MagPI is a suitable method for recording changes in sediment surface adhesion using magnetic attraction with either permanent magnets or electromagnets (Larson et al., 2009). In the present study, the magnetic source used to attract the particles was the purpose-made electromagnets constructed using a metal core of ferrous alloy coiled with an insulated copper thread. The electromagnets were controlled by a fine and precise variation of voltage and current from a power supply. A small amount of ferromagnetic fluorescent particles were distributed on the sediment surface. To ensure a roughly single layer of particles, a cut-off 2 mL syringe, submerged into the water and held closely to the surface was used to guide the deposition of the particles after being introduced into the water through a plastic pipette. Immediately, the magnetic core was lowered to a distance of 10 mm from the surface, achieved from the tip of a plastic rod attached at the end of a metal core. The magnet was lowered until the plastic rod just touched the sediment surface. A magnifying glass and video camera connected to a screen were used to aid the visual observation (Figure 4). The voltage applied to the electromagnets was gradually increased, and recorded when all particles were removed.

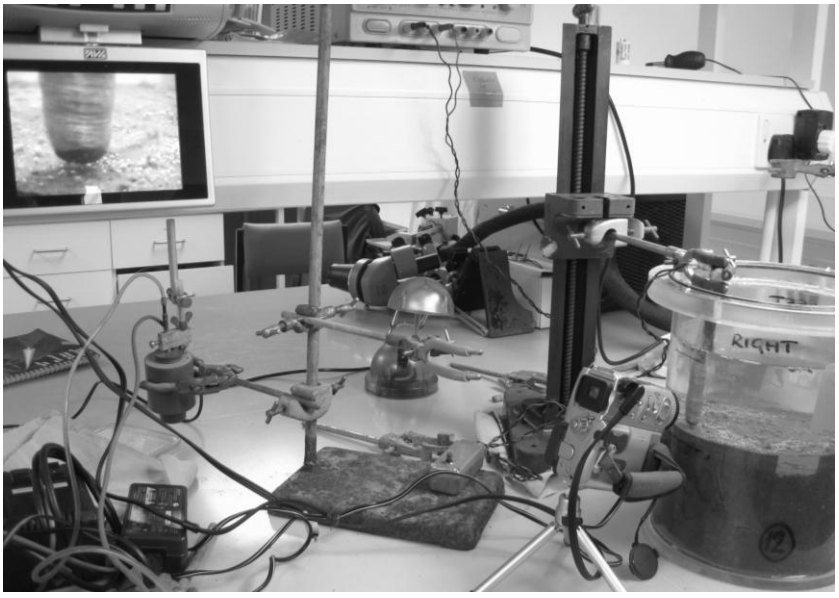

Figure 4. Measuring surface adhesion using a MagPI. On the right hand side of the figure, the magnetic rod is being lowered to a set distance from the sediment surface. Particle removal was recorded using a video camera and displayed on a screen for an easier view.

Calibration of the device was done by placing the magnet over a sensor connected to a Gauss meter at a set distance of 10 mm. Small increments of voltage (0.2 V) and

current (0.1 A) were applied and the magnetic flux density (MFD – unit: mTesla) for each increase was recorded. Calibration was performed in three replications with the probe submerged in seawater. A strong linear relationship (r = 0.995) between the voltage and MFD was recorded (Figure 5). Measurement of the adhesive property of the sediment surface was calculated from the linear line equation obtained in the calibration based on the voltage at which all particles were removed.

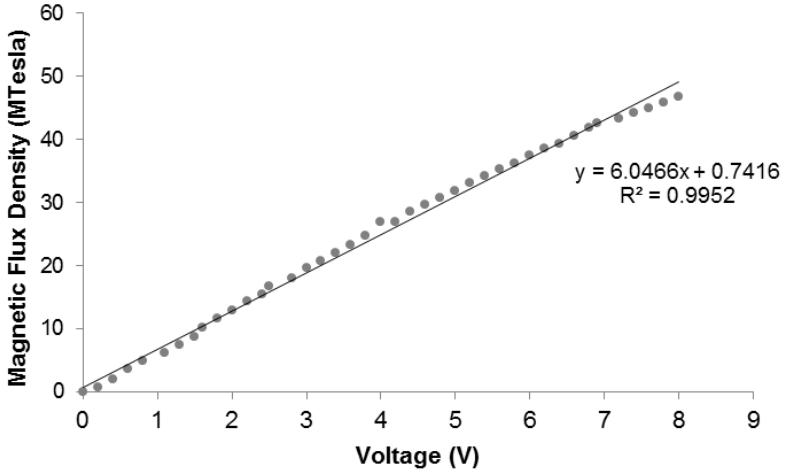

Figure 5. Calibration curve of measurement between MagPI probe and a sensor connected to a Gauss meter.

Low Temperature Scanning Electron Microscopy (LTSEM)

LTSEM has been extensively used to analyse the structure of biofilms and microbial mats in sediment (Perkins et al., 2006) and relate their quality to sediment stability (Paterson et al., 1998, Black et al., 2001). The frozen samples for LTSEM analysis were placed into a cryro-apparatus. At this stage, the samples were freeze dried to remove any remaining surface water before images were taken. A more detailed method for the examination of frozen sediment under LTSEM is described by Paterson (1995). *Note: due to unforeseen technical problems, this microscopy procedure had to be modified which meant the samples were freeze-dried separately in a freeze-drier. The samples were completely dried and therefore the imagery is considered as Scanning Electron Microscopy (SEM).*

Microphytobenthic assemblage

The composition of live and dead cells of the microphytobenthic community was assessed from the same samples used for LTSEM. The frozen samples were defrosted and diluted in distilled water in Eppendorff tube. Up to 300 cells of dead

and live diatoms and cyanobacteria were counted and classified into the following size-classes: < 30 µm, 30 – 100 µm, and > 100 µm. In addition, the colonial cells were also recorded. All identifications were carried out using a compound microscope.

Statistics

Prior to univariate analysis, all results were tested for assumptions of normality and homogeneity of variance (visual assessment and Bartlett test), and the assumptions were fulfilled. A paired samples t-test was applied on data in the control tank to test the difference between replications of different sampling dates. A Two-way Analysis of Variance (Two-way ANOVA) was used to test the difference of individual sediment characteristics between different treatments and flow conditions. The relationship between individual sediment properties was tested using the Pearson correlation coefficient.

Multivariate tests were carried out using PRIMER package version 6 (Clarke and Gorley, 2006). Principle coordination analysis (PCA) was used to determine the influence of sediment properties on sample distribution. Non-parametric multi-dimensional scaling (MDS) ordination using the Bray-Curtis similarity measure was applied on all treatments to test for differences in overall sediment properties between treatments and flow conditions. The distance between samples on the ordination explains the similarity of data where the clustered samples are more similar than the dispersed samples. Analysis of similarity (ANOSIM) was used to test the significant difference between treatments and between different flow conditions. The value (R-value) from this test ranging from -1 to 1 where the value close to 0 indicates the high similarity between samples, while the value close to 1 indicates the samples are different. A negative value is produced when the similarity between samples is higher than the similarity within samples. The MDS was also used to determine the differences in microphytobenthos assemblages between tanks. All analyses were performed with the sediment properties as normalised variables.

Results

Visual observations

After 2 days incubation period, surface biofilm was visible in patches in all tanks (control and treatments). Then, another 2 days after *H. diversicolor* was introduced, the patches of biofilm were substantially reduced especially in the tanks containing the worms. In addition, these tanks also showed some visible mucous strings created by the worm. Mortality rate was determined by comparing the number of worms introduced (day 1) and the number recovered on day 4. The highest mortality was recorded for the treatment S with 38.5% ± 43.6 (low flow) and 41.4% ± 5.0 (high flow). This was followed by the treatment M with 23.0 ± 5.1 (low flow) and 32.9.0% ± 5.2 (high flow). The treatment L recorded the lowest mortality rate with only 14.3% ± 11.6 (low flow) and 22.0% ± 8.6 (high flow).

Individual sediment properties in low and high flow intensities

Generally, the individual sediment properties in control tanks and between different replications were not significantly different (T-test: $p > 0.05$) (Appendix 1a). This suggests that the results from this study were not an artefact of different times for the replications.

The presence of worms and the different flow rates showed some effects on sediment properties. The most pronounced difference was recorded for organic content where a significant difference was recorded for treatments and flows (Figure 6). For example, the presence of *H. diversicolor* of different body sizes significantly changed the organic content (two-way ANOVA: $p = 0.00$, df = 3). In addition, a pair-wise comparison also showed a significant difference where in day 1, treatments S and M were higher in organic content compared to treatments L and C (Tukey post-hoc test: $p = 0.00$). With the exception of day 2, the difference was significant for the entire period of study where the treatments S and M contained the highest amount of organic material while the treatment C contained the lowest amount (Tukey test: $p < 0.05$). This trend however, changed under the high flow condition. In day 1, treatments S and C were higher in organic content compared to other treatments. A pronounced decreased recorded in day 4 for all but treatment C which was significantly higher (Tukey test: $p < 0.05$). Significant change in organic content was also recorded with the low flow giving a higher organic content (two-way ANOVA: $p <$

0.05) except for the treatment C. The differences between treatments and flow conditions were observed for the entire period of sampling.

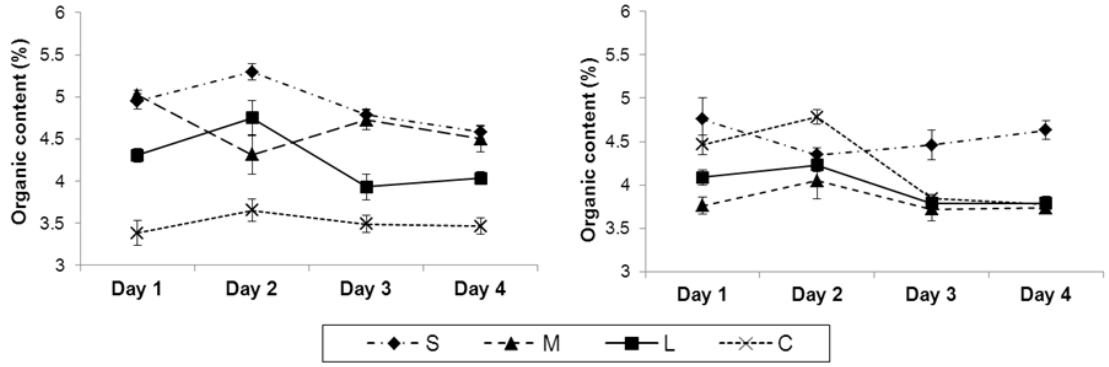

Figure 6. Mean values (± confidence intervals) of organic content over the course of the experiment under low (left) and high (right) flow intensities.

The effect *H. diversicolor* on colloidal carbohydrate concentration was only observed in the presence of large-bodied worms and only on day 1 and day 2 (Figure 7). Treatment L was significantly lower in carbohydrate compared to the other treatments (Tukey test: $p < 0.05$). Significant difference between flow conditions for carbohydrate was recorded on day 2 and 4 with the concentration of carbohydrate higher in low flow condition for all treatments (2-way ANOVA: $p < 0.05$).

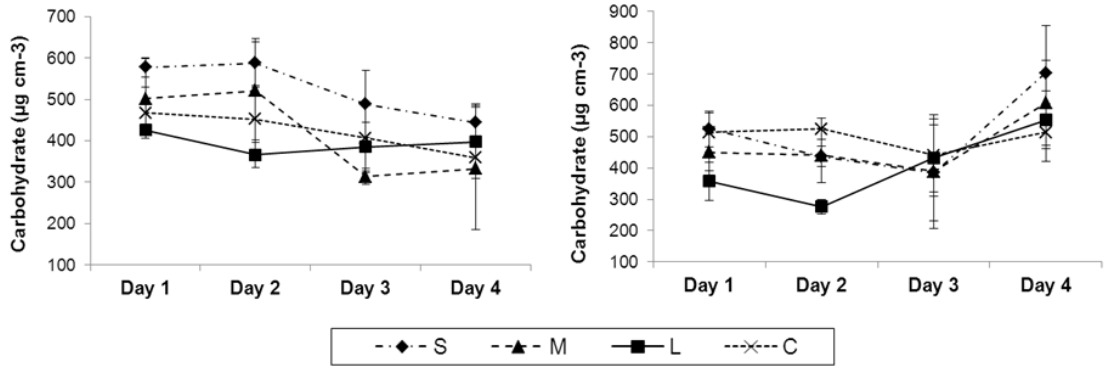

Figure 7. Mean values (± confidence intervals) of colloidal carbohydrate concentrations over the course of the experiment under low (left) and high (right) flow intensities.

Colloidal protein concentration recorded no significant difference between treatments for both flow conditions on all days (Tukey test: $p > 0.05$) (Figure 8). Comparison between flows showed that low flow intensity was higher in protein concentration than

under high flow for both days and in all treatments (2-way ANOVA: $p < 0.05$) except in treatment S.

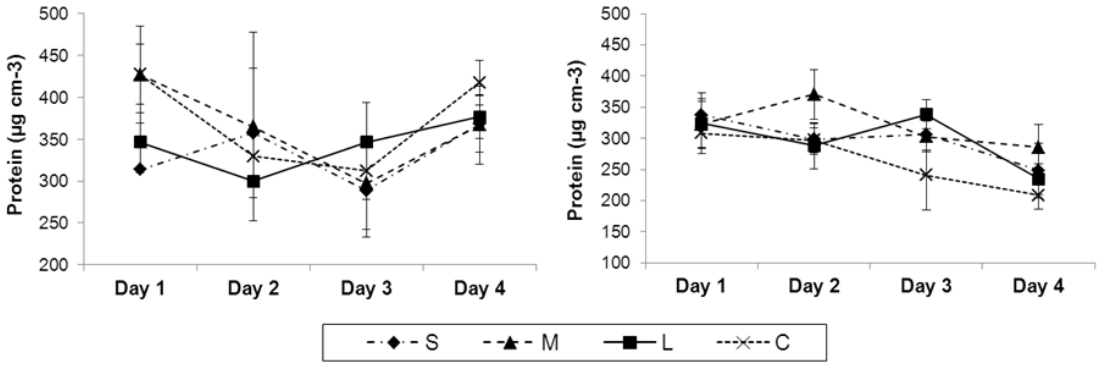

Figure 8. Mean values (± confidence intervals) of colloidal protein concentrations over the course of the experiment under low (left) and high (right) flow intensities.

Chlorophyll-a concentration was similar for all treatments under both flow conditions (Tukey test: $p > 0.05$) (Figure 9). The difference between flows was only recorded on day 1 where this property was lower under low flow than the high flow conditions (2-way ANOVA: $p < 0.05$).

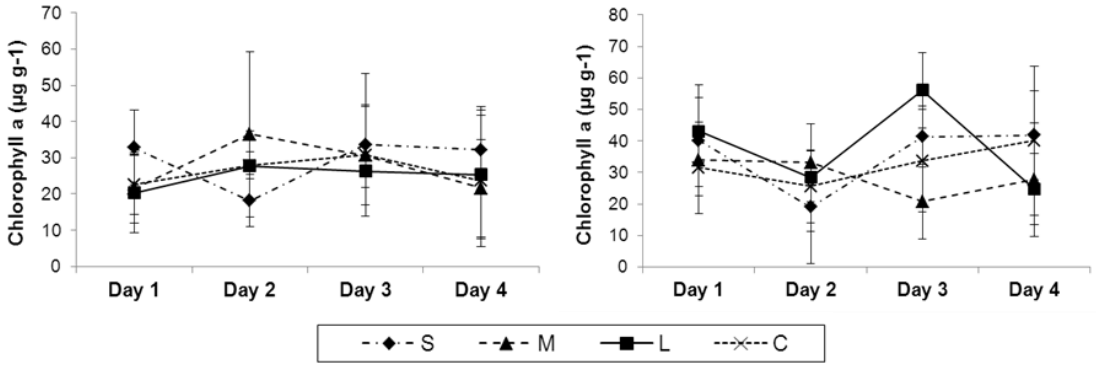

Figure 9. Mean values (± confidence intervals) of chlorophyll-*a* concentrations over the course of the experiment under low (left) and high (right) flow intensities.

The difference of water content between treatments was only recorded on day 1 under low flow condition (Figure 10). Treatment M was higher in water content than in the control tank (Tukey test: $p < 0.05$), while no difference was recorded for other treatments (Tukey test: $p > 0.05$). The difference between flow conditions was

recorded only on day 4 where the water content was higher under high flow condition (2-way ANOVA: $p < 0.05$) except in treatment L.

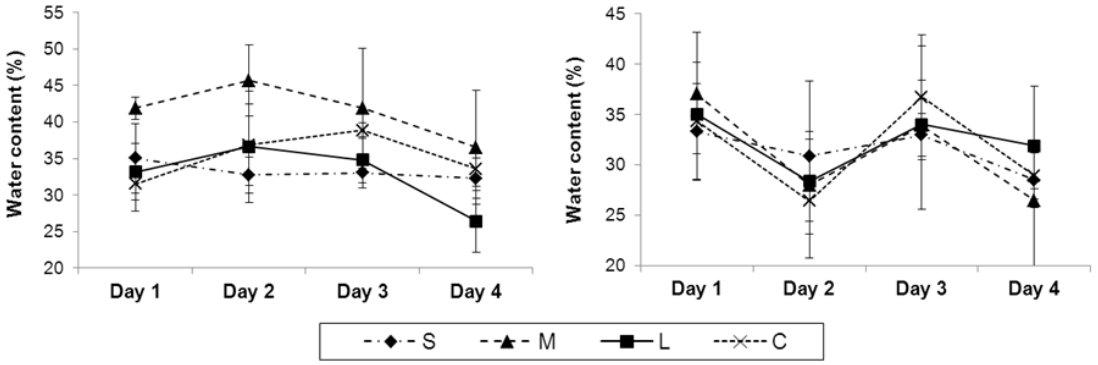

Figure 10. Mean values (± confidence intervals) of water content over the course of the experiment under low (left) and high (right) flow intensities.

As in the water content, the difference in dry bulk density was also recorded for treatment M on day 1 under low flow condition (Figure 11). This treatment was lower compared to other treatments (Tukey test: $p < 0.05$). Comparison between flow condition showed that sediment under high flow condition showed a higher bulk density for all sampling days (2-way ANOVA: $p < 0.05$).

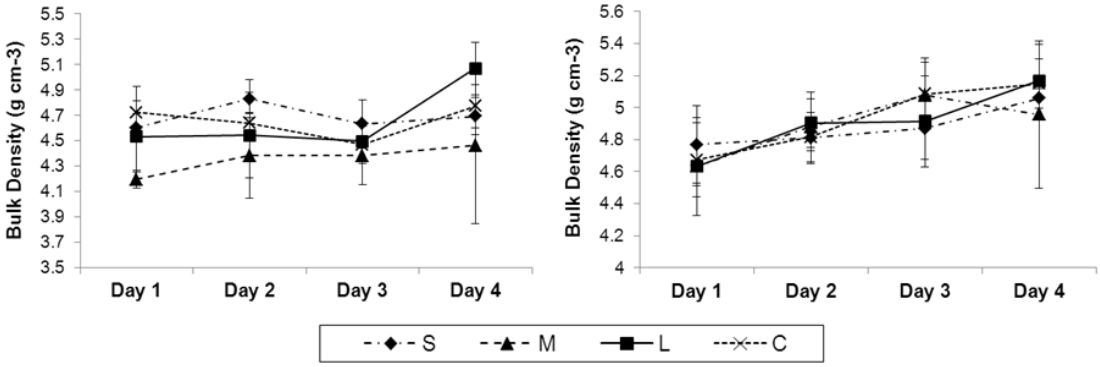

Figure 11. Mean values (± confidence intervals) of dry bulk density over the course of the experiment under low (left) and high (right) flow intensities.

Relationship between sediment properties

There was in general a poor relationship between sediment properties. Out of 15 possible pairings, only 2 pairs of sediment properties recorded a significant correlation. A positive correlation was recorded between colloidal carbohydrate and

dry bulk density (Pearson correlation, r = 0.369, $P < 0.05$) while a negative correlation was recorded between water content and dry bulk density (r = -0.785, $P < 0.05$). The PCA indicated that the effect of the flow intensity on individual sediment properties in day 1 can be seen only in control tank (Figure 12a). Under low flow condition, the properties of the control tank were mainly influenced by bulk density. The treatment tanks were mostly influenced by organic content and chlorophyll *a*. Samples taken under high flow condition showed less difference between control and treatments tanks where samples were mainly influenced by chlorophyll *a* and organic content. Principle component 1 and 2 account for 56.7% of total variability between the samples. Samples in day 4 showed a more pronounced effect of the flow intensity (Figure 12b). Samples under low flow condition were mostly influenced by colloidal protein, organic content and chlorophyll *a.* The control tank showed a fairly clear separation from other treatment tanks. Within the treatments, samples from the treatment S (mostly influenced by organic content) recorded a pronounced difference from the treatment L which mostly influenced by chlorophyll *a*. The difference was less pronounced for samples in treatment M. Meanwhile, samples under high flow condition were mostly influenced by chlorophyll *a* and bulk density. Samples from control and treatment S were grouped together and mostly influenced by chlorophyll *a*. Another group was shown between samples from treatments M and L which were mostly influenced by bulk density. Principle component 1 and 2 account for 66.6% of total variability between the samples.

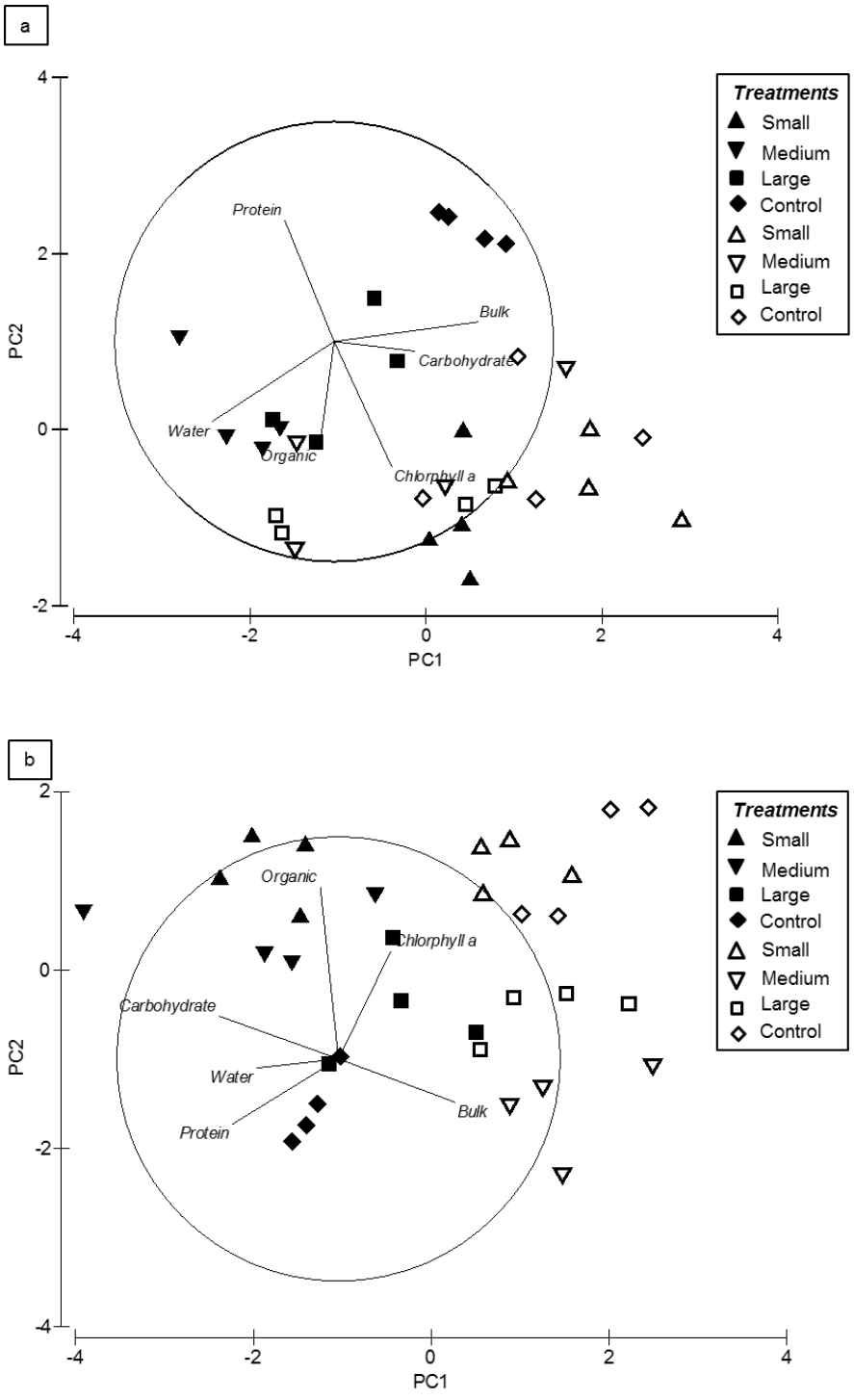

Figure 12. PCA of the sediment properties from all treatments in both low and high flow conditions on day 1 (a) and day 4 (b). Samples are distributed in relations to measurement of organic content, colloidal carbohydrate, colloidal protein, chlorophyll *a*, water content and bulk density. Shaded symbols correspond to low flow and open symbols correspond to high flow condition.

Overall sediment properties comparison

Multivariate analysis using MDS indicated differences of overall sediment properties between treatments. On day 1, samples under low flow condition showed little evidence of similarity between treatments judging from the dispersal of samples (Figure 13a). Treatments S and C showed the most obvious difference from other treatments. Samples from treatments M and L were more similar to each other where two individual samples from both treatments grouped together. Sediment properties under high flow condition were less clustered on the ordination. Unlike in the low flow condition, the sediment under high flow showed no difference between control and other treatments. With the exception of treatment S under low flow condition, samples from different flow conditions varied in the overall sediment properties. The difference between samples under different flow conditions were more pronounced in day 4 (Figure 13b). Under low flow condition, the control still showed an evidence of dissimilarity from other treatments. However, this difference was lessened under high flow condition as the control tank was more similar to the treatment S. The general dissimilarity between treatments in both flow intensities was confirmed by the high R-value from the ANOSIM tests (Table 1). Sediment properties between treatments were significantly different at $p < 0.05$, both at the start and at the end of the experiment. The ANOSIM also showed that the difference between treatments was reduced from day 1 to day 4 of the experiment. However, the difference between flows increased in day 4.

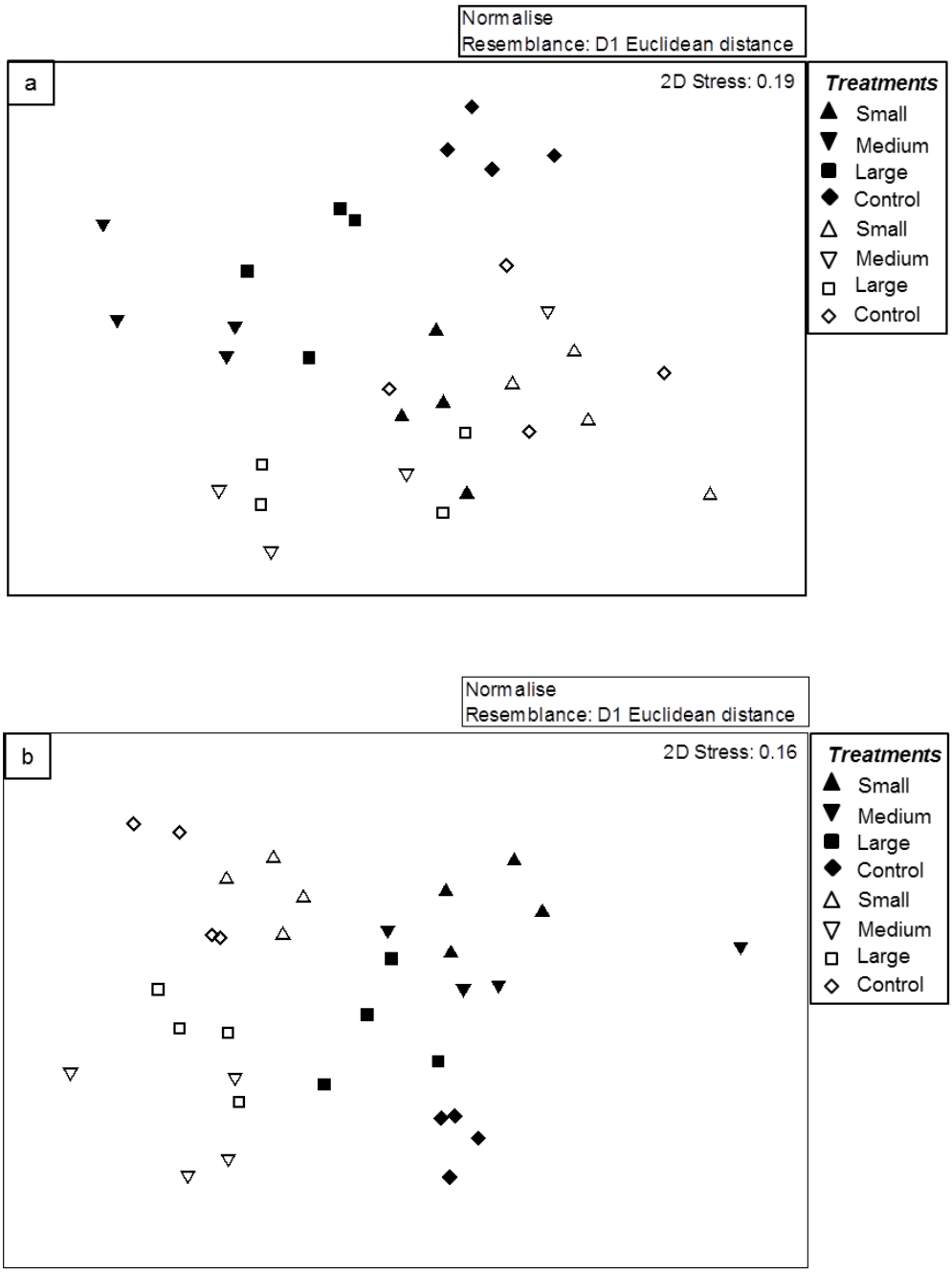

Figure 13. MDS from the normalised data of the sediment properties from all tanks in both stable and disturbed conditions, on a) day 1 and b) day 4. Samples are distributed in relation to measurement of organic content, colloidal carbohydrate, colloidal protein, chlorophyll *a*, water content and bulk density. Shaded symbols correspond to low flow and open symbols correspond to high flow condition.

Table 1. Comparison of sediment properties between treatments and flows using two-way ANOSIM test. All data showed a significant difference at $p = 0.05$ as shown in bold.

	R-value	*p* value
Day 1		
Global R		
Treatment	**0.697**	**0.001**
Flow	**0.719**	**0.001**
Pairwise test		
S v M	**0.823**	**0.002**
S v L	**0.896**	**0.001**
S v C	**0.625**	**0.007**
M v L	**0.495**	**0.014**
M v C	**0.672**	**0.002**
L v C	**0.625**	**0.005**
Day 4		
Global R		
Treatment	**0.523**	**0.001**
Flow	**0.924**	**0.001**
Pairwise test		
S v M	**0.495**	**0.006**
S v L	**0.745**	**0.002**
S v C	**0.510**	**0.011**
M v L	**0.234**	**0.053**
M v C	**0.703**	**0.003**
L v C	**0.568**	**0.006**

Sediment stability

The stability of the sediment surface showed a general trend that the adhesive capacity reduced under higher flow intensity (Figure 14). Statistical tests revealed that in day 1, the difference was not significant between treatments (Table 2, 3). The differences were significant in day 4 between treatments (two-way ANOVA: $p = 0.042$, df = 3) and flows ($p = 0.000$) (Table 4). A pairwise test revealed that the only difference was between treatment M and control (Tukey post-hoc test: $p = 0.05$) where the control tank had a significantly higher adhesive capacity (Table 5).

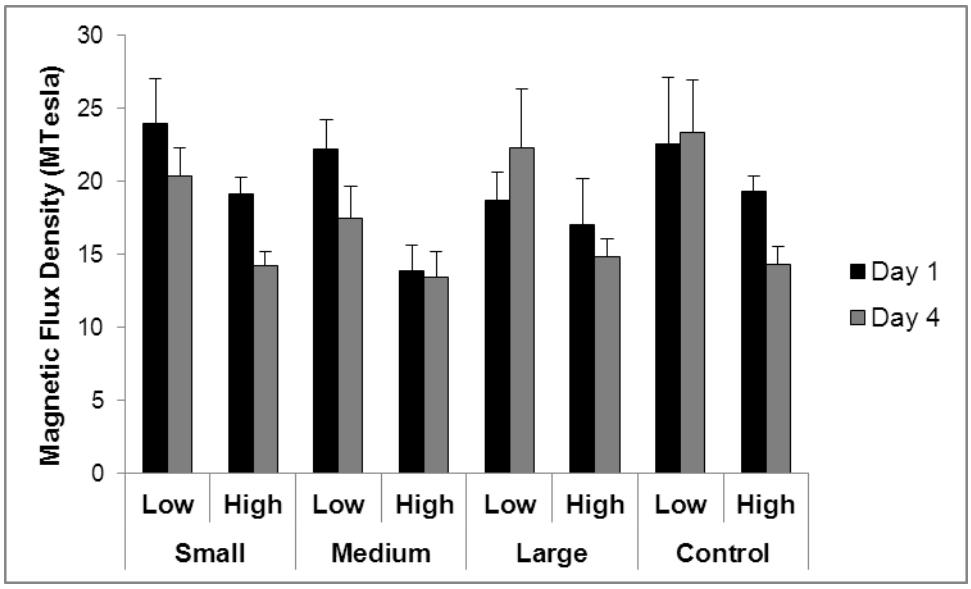

Figure 14. Adhesive capacity of the sediment as measured by MagPI between treatments and flow conditions. Data presented for first and final day of sampling.

Table 2. Two-way ANOVA comparison of MagPI between treatments and flows in day 1. Significant difference indicated in bold.

	d.f	F value	*p* value
Treatment	3	1.669	0.200
Flow	1	0.796	0.381
Interaction	3	2.982	**0.050**

Table 3. Tukey post-hoc test for pair-wise comparison of MagPI between treatments in day 1. No significant difference was recorded.

p value			
	S	M	L
M	0.480		
L	0.729	0.975	
C	0.952	0.223	0.416

Table 4. Two-way ANOVA comparison of MagPI between treatments and flows in day 4. Significant difference indicated in bold.

	d.f	F value	*p* value
Treatment	3	3.177	**0.042**
Flow	1	60.373	**0.000**
Interaction	3	1.501	0.240

Table 5. Tukey post-hoc test for pair-wise comparison of MagPI between treatments in day 4. Significant difference indicated in bold.

p value			
	S	M	L
M	0.471		
L	0.707	0.078	
C	0.582	**0.050**	0.997

Microphytobenthos assemblage

The similarity in microphytobenthos assemblages between samples was analysed by means of an MDS ordination. Samples in day 1 were fairly well separated between different treatments and flow intensities (Figure 15a). However, the R-value of ANOSIM revealed that the only significant difference was between treatment L and control tank (Table 6). The difference was not observed on day 4 judging from no clear trend of grouping in the MDS (Figure 15b) and generally low R-value (Table 6). The similarity in microphytobenthos assemblages across treatments was also confirmed by the SEM images, which show that all samples are characterised by the presence of mixed microphytobenthos assemblages with a visible EPS matrix (Figure 16).

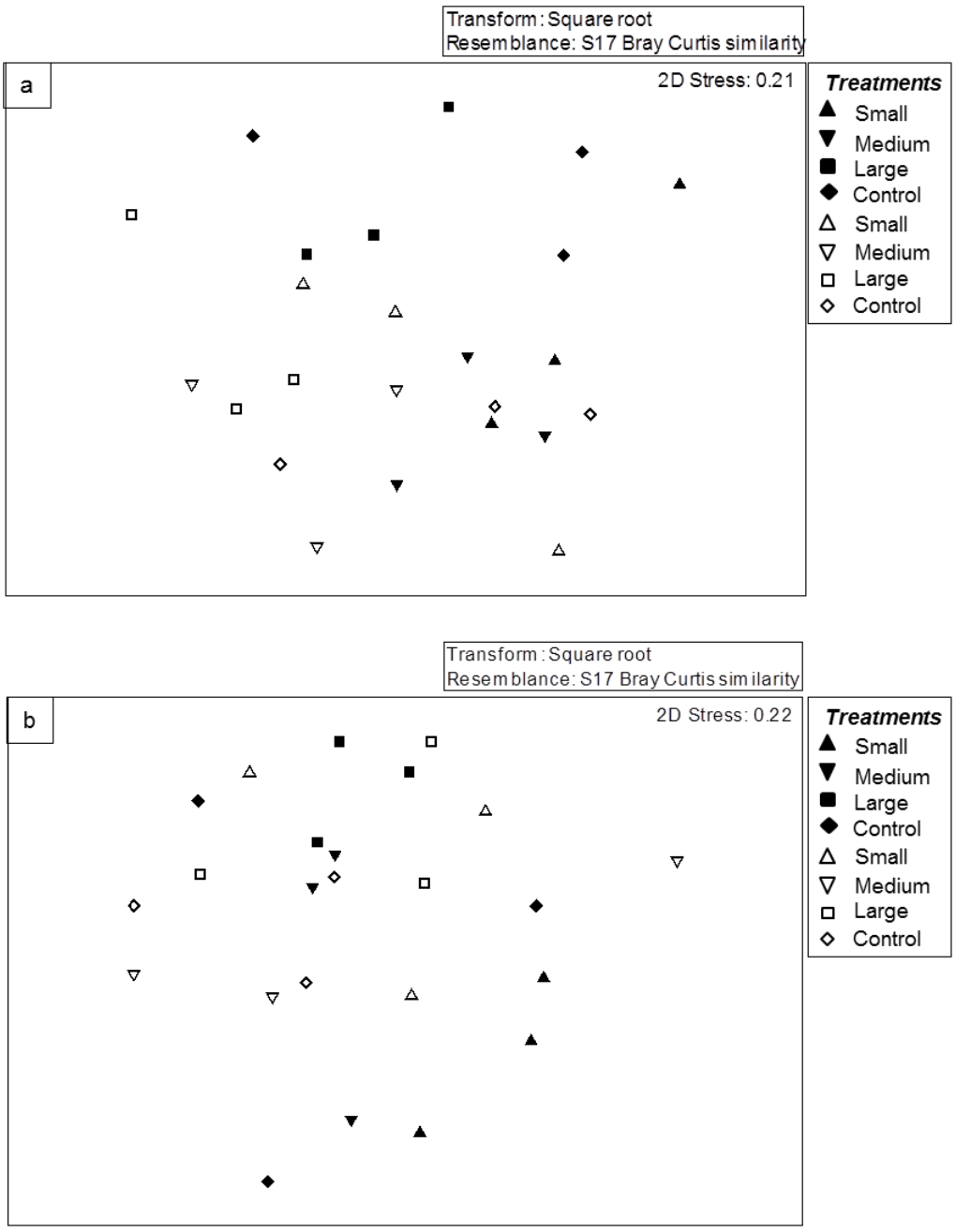

Figure 15. MDS of microphytobenthic assemblage in different treatments and flow intensities, on a) day 1 and b) day 4. Shaded symbols correspond to low flow and open symbols correspond to high flow condition.

Table 6. Comparison of microphytobenthic assemblage between treatments and flows using two-way ANOSIM test. Significant difference (at $p = 0.05$) in bold.

	R-value	*p* value
Day 1		
Global R		
Treatment	**0.233**	**0.021**
Flow	**0.315**	**0.040**
Pairwise test		
S v M	-0.074	0.760
S v L	0.463	0.080
S v C	0.019	0.430
M v L	0.278	0.090
M v C	0.241	0.160
L v C	**0.407**	**0.010**
Day 4		
Global R		
Treatment	-0.009	0.511
Flow	-0.046	0.681
Pairwise test		
S v M	0.241	0.190
S v L	0.278	0.140
S v C	-0.093	0.780
M v L	0.037	0.290
M v C	-0.185	0.910
L v C	-0.222	0.930

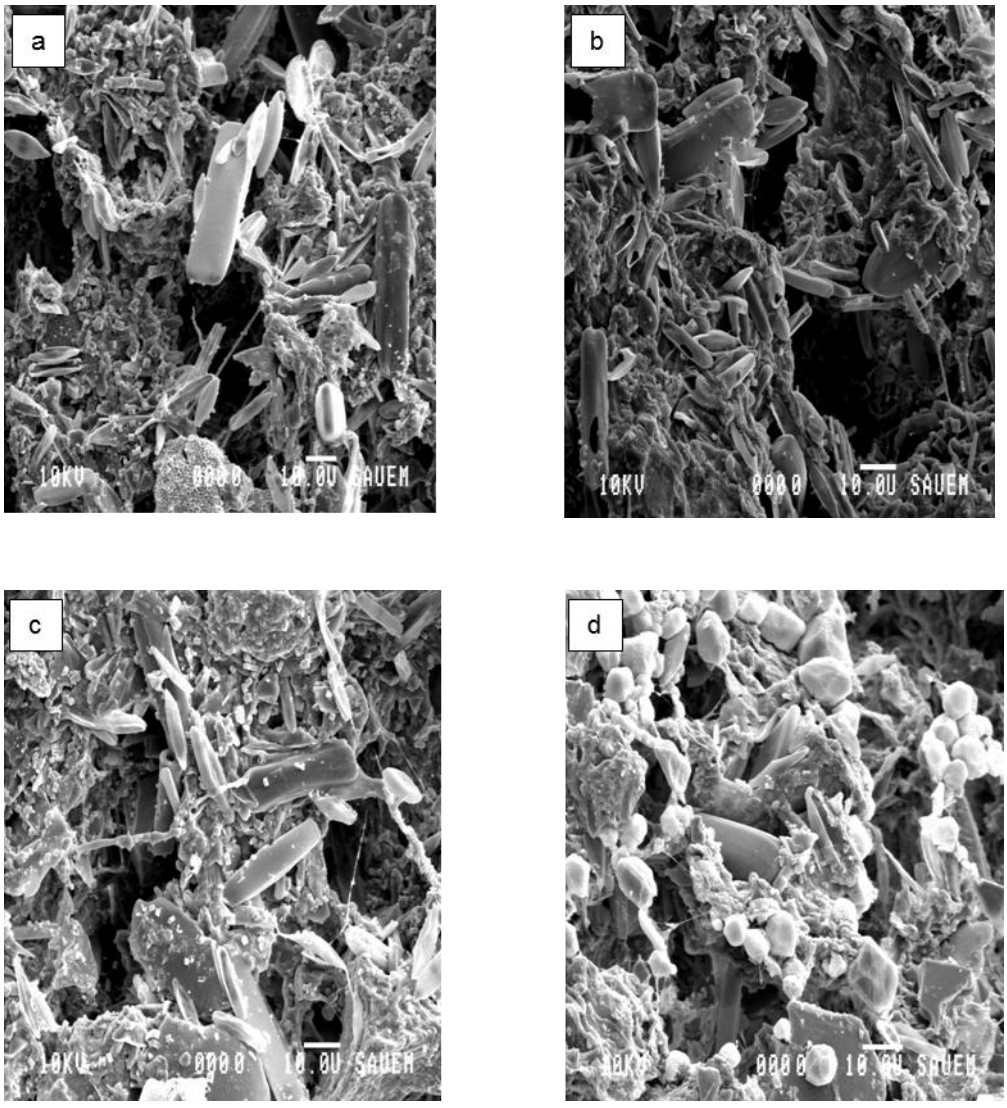

Figure 16. SEM images of all tanks using similar magnification showing microphytobenthos assemblages covered in an EPS matrix in A) treatment S, B) treatment M, C) treatment L, D) control tank.

Discussion

Several studies on the effect of *Hediste diversicolor* on sediment stability have been carried out in intertidal sediments with different conclusions. Meadows and Tait (1989) and Meadows et al. (1990) showed that *H. diversicolor* improved sediment stabilisation. Yet, both field and laboratory experiments have also shown that the presence of this worm decreased the sediment stability (de Deckere et al., 2001; Underwood and Paterson, 1993; Widdows et al., 2006). They concluded that the feeding mechanisms (burrowing and surface deposit feeding) of the worm may have increased sediment resuspension and thus the erosion rate. Other than that, the

increase of the erosion rate might also the product of an increase in bottom roughness through tube building by the worm (de Deckere, 2003).

The most pronounced effect of the presence of *H. diversicolor* and its different body sizes was recorded for organic content. As shown on day 1 and day 4, the presence of *H. diversicolor* increased the organic content. This is believed to be due to galleries built by the worms which helped to increase the sediment consolidation (Meadows and Tait, 1989; Murray et al., 2002), which in turn, prevent the sediments from eroding that causes the reduction in organic matter (Fernandes et al., 2006). However, this trend changed under high flow condition where the presence of this worm substantially decreased the organic content. This showed that the tube galleries built by these worms were not able to protect against the high flow rate. Carbohydrate content showed a significant difference where this sediment property in treatment L (day 1) was significantly lower than in the other treatments. Although only involving the large body sized worm, this finding was at least consistent with other studies which suggest the grazing activity of *H. diversicolor* (Vedel and Riisgård, 1993; Paramor and Hughes, 2004, Engelsen and Phil, 2008) reduced the surface biofilm (Miller et al., 1996; Austen et al., 1999). The effect of grazing activity was also apparent in terms of microphytobenthos assemblage where a higher effect was recorded in the treatment L compared to the other treatments (Table 7.7).

The effect of flow conditions was important for most of the sediment properties. Most of the properties were higher under low flow condition with several exceptions especially for dry bulk density and chlorophyll *a*. The high dry bulk density under high flow condition was not anticipated as it is assumed that the high flow might reduce the sediment compaction, hence decrease dry bulk density (Flemming and Delafontaine, 2000). Meanwhile, it could be argued that the compaction of the sediments which result in high bulk density (i.e. less spaces between particles, hence the sediments are more stable) should reduce the chlorophyll *a*, and vice versa (Perkins et al., 2003). This is based on the basis that compaction increases the amount of sediments within a set volume, hence the sample collection would include the sediment from deeper layers which are normally less rich in chlorophyll *a* (Kelly et al., 2001). However, this is not the case in the present study where chlorophyll *a* also increased under higher flow intensity. In fact, there was no correlation between these

properties. Therefore, the increase of chlorophyll *a* was more likely to be due to other reasons, which might include a decrease in grazing activity.

The importance of microphytobenthos as sediment biostabiliser has been well documented (e.g. Paterson, 1989; Underwood and Paterson, 1993; Sutherland et al., 1998; Paterson and Black, 1999) and their high density was found to be a vital factor that increases the critical erosion threshold of natural sediments (Sutherland et al., 1998). Microphytobenthos produces cellular exudates, namely extracellular polymeric substances (EPS) which come in the form of mucus-like carbohydrates that help in binding the sediment particles and thus increase the erosion threshold (Widdows and Brinsley, 2002). In the present study, the microphytobenthos assemblages did not change with the presence of the worms, suggesting that the grazing activity of *H. diversicolor* had no impact on these assemblages. This finding was in accordance with others studies which reported that although having a large body, *H. diversicolor* has relatively low effect on MPB biomass compared to other smaller-bodied fauna such as *Corophium volutator* and *Hydrobia ulvae* (Dyson et al., 2007; Ieno et al., 2006; Nizzoli et al., 2007). The lack of difference in microphytobenthos assemblage was reflected by the adhesive capacity of the sediment. The MagPI study showed that the adhesive capacity of the biofilm was not significantly different between different treatments and flow intensities. According to Lubarsky (2011), the strength of adhesive capacity of biofilm depends on the species composition which comprises different colonisation strategies and EPS origin.

In general, the presence of *H. diversicolor* did not affect sediment properties in this study. Where there were significant effects, the difference trend did not explain the (de)stabilising factors. Likewise, the difference in overall sediment properties between all treatments and control did not indicate whether *H. diversicolor* stabilised or destabilised the sediments. This finding was not anticipated as it opposes the findings by other authors about the effect of the presence of this worm, regardless of its body size. There are several possible factors that minimised the effect of this species on sediment stability in the present study, one being the size of the mesocosm system. The present study used small circular tanks with a capacity of only 3.8 L compared to other laboratory studies with larger (~60 L) tanks (Fernandes et al., 2006) and flume (Widdows et al., 2009), which did show significant changes in sediment stability by the presence of *H. diversicolor*. It is also acknowledged that work by Biles et al.,

(2003) which used similar tanks as in the present study recorded significant effect by *H. diversicolor.* However, this study examined different variables, namely nutrient fluxes in the water column which are possibly more sensitive to any change than the bulk sediment characteristics. The lack of tidal cycle could also play a part in the results of the present study. This is due to the tendency of the worms to remain in their burrows at high tide (Esselink and Zwarts (1989). The constant submersion of the sediment in the present study might have reduced the impact of the worms' activity on the sediment stability. However, this method was also applied in other experiments with different outcomes (e.g. Biles et al., 2003; Fernandes et al., 2006; Dyson et al., 2007), thus suggesting that this factor might have a limited impact. The tank size factor could also have an effect on oxygen concentration and distribution. According to Pischedda et al. (2012), one of the main factors that control the oxygen diffusion is the distance from the sediment-water interface. Since the depth of the sediment in the present study was too shallow (as opposed to the depth of *H. diversicolor* burrow in natural environment), the effect of oxygen diffusion might not have been detected.

The mortality rate was positively correlated with the worm density. This could be due to the effect of an increased stress in a denser community. Mortality rates of *H. diversicolor* are, however, believed to be a non-causative factor of the findings of the present study as these were lower than recorded by Fernandes *et al*. (2006), where a significant effect of the presence of *H. diversicolor* on the sediment stability was recorded.

Conclusions

There is no consensus among biologists with regard to the effect of *H. diversicolor* on the sediment stability. Previous studies in the 1990s suggested a biostabilising effect by the worm through the production of mucous glands that help bind the sediment together. More recent studies suggested on the contrary that the bioturbation activity of this organism increases sediment erosion rates. In addition, other bioturbatory species such *as Macoma balthica* and *Hydrobia ulvae* have been reported to destabilise sediment (Widdows et al., 2000a; b; Andersen, 2001). The present study found out that in general, the presence of *H. diversicolor* did not affect the measured sediment characteristics and sediment stability. Different body sizes of the organism also showed no influence in changing the sediment environment. However, changes

were detected when the sediment was exposed to flow disturbance. This finding was in accord to many studies which have reported the detrimental effects of physical disturbance on benthic ecosystems. Larger tank capacity is perceived to be a more appropriate mesocosm system in detecting the effect imposed by macrofauna.

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